# BIOSYSTEMATICS OF INSECTS LIVING IN FEMALE BIRCH CATKINS. I. GALL MIDGES OF THE GENUS *SEMUDOBIA* KIEFFER (DIPTERA, CECIDOMYIIDAE)

by

J. C. ROSKAM

*Division of Systematics and Evolutionary Biology, University of Leiden, The Netherlands*

With 122 text-figures

ABSTRACT

Five species of *Semudobia* Kieffer have been studied in their developmental stages. All stages are described and keys are provided. A neotype is designated for *Cecidomyia betulae* Winnertz, 1853, from *Betula pendula* (fruit galls), The Netherlands, and four new species are described, viz., *Semudobia brevipalpis* from *Betula papyrifera* (fruit galls), Canada, Quebec; *S. steenisi* from *B. occidentalis* (fruit galls), U.S.A., Wyoming; *S. tarda* from *B. pendula* (fruit galls), The Netherlands; and *S. skuhravae* from *B. pendula* (bract galls), The Netherlands.

## INTRODUCTION

In this paper, the first of a series on the entomofauna of female birch catkins, the galls, morphology and life cycle of five species of gall midges of the Holarctic genus *Semudobia* Kieffer are studied. In a second publication, now in preparation, morphology, life cycle and host relations of some of the hymenopterous parasites of these midges will be discussed. Finally, a "food web" will be constructed and attention will be paid to phylogenetic aspects of host-parasite relations of the species under study.

The first description of *Semudobia betulae* was published by Winnertz in 1853. He placed it in the genus *Cecidomyia* Meigen. Rübsaamen (1891) transferred the species to his genus *Hormomyia*. Kieffer (1895) originally placed it in the genus *Oligotrophus* Latreille, but in 1913 he made it the type-species of a new genus *Semudobia*. Although a rather recent review was given by Barnes (1951), it is necessary to discuss the literature in detail on certain topics. In fact these topics anticipate the splitting of the only described species in the genus.

Data on the number of antennal segments. — A mistake was made in the original description by Winnertz (1853). Although there may be some variation in the number of segments of the flagellum, the formulae 2 + 10/11 in the males (2 means scape plus pedicel, the other number is given for the segments of the flagellum) and 2 + 10 in the females, as indicated by Winnertz, are highly uncommon in *Semudobia*. Löw (1878) critisized these numbers, but unfortunately his counts (males 2 + 12, females 2 + 13) do not fit either, because males in

*Semudobia* usually have one segment more than females. Barnes (1951) had also problems with the number of antennal segments, as for the females he recorded 2 + 12, "but occasionally (—) 2 + 15", which must be an error for 2 + 13. The data given by Rübsaamen (1891), Theobald (1892) and Kieffer (1913b) are correct: 2 + 12/14 (♂), 2 + 11/13 (♀).

Gall inducing and gall form. — Winnertz described *C. betulae* after specimens reared by Kaltenbach from female catkins of *Betula alba* L. from the preceding year. Neither Winnertz (1853) nor Kaltenbach (1874) did note that the midge was a gall inducer. In fact, the statements by Kaltenbach (1874) and Binnie (1877) are very confusing. They reported that the larvae live and pupate "in the interstices between the scales", although Binnie also observed the "inside of a seed" as a common position of the larva. Löw (1878), and later Wachtl (1881), were the first to study the behaviour of *Semudobia* carefully.

Löw critisized Kaltenbach (1874) heavily, considering "diesbezügliche Beobachtungen als äusserst oberflachlich", and observed the larvae of *Semudobia* enclosed in galls. Löw and Wachtl both described the galls; they reported at least two different gall forms but did not attribute these to different gall inducing species. Rübsaamen (1891) added a third gall form to those described by Löw and Wachtl, but did not suppose it to be due to a different gall inducing species either. A remarkable mistake was made by Connold (1901, 1909), when he stated *Semudobia* to be responsible for deformations of male birch catkins! These deformations are not rare indeed and most causes were listed by Gäbler (1958). The deformations of female catkins, attributed to *Semudobia* by Swanton (1912), are doubtful too. Rübsaamen & Hedicke (1925—1939) figured the three different gall types (pl. XXV figs. 1—4) but again considered them to belong to one gall midge species. The only authors, who realized the different gall forms in female birch catkins to be due to different species, were Skuhravá & Skuhravý (1960, 1963).

Besides the gall inducing midges belonging to the genus *Semudobia* other gall midges, inquilines, and phytosaprophagous midges may be found in the fruit catkins of *Betula*. At least two, not identified, species of inquiline gall midges are common in the galled catkins and may occasionally pupate "in the interstices between the scales". So it seems probable that these inquilines were observed by Kaltenbach (1874) and Binnie (1877). Suggestions about the identity of these larvae were discussed later by Thomas (1893), Escherich (1942) and Skuhravá & Skuhravý (1963). Hodges (1969) reported *Clinodiplosis* sp. as an inquiline midge. Larvae of this genus are indeed frequent inhabitants of fruit catkins of *Betula*, but there is no correlation between the occurrence of this midge and the presence of *Semudobia* galls. *Clinodiplosis* is common in the "deformed and dwarfed catkins" described by Swanton (1912) and is supposed to be a fungus eater in these catkins (Skuhravá, 1970).

Larval characters. — Papillae of *Semudobia* larvae were studied by Rübsaamen (1892), Kieffer (1895) and Möhn (1955). Phase-contrast microscopy being unknown or uncommon in those days, it is not surprising that their data are very incomplete and not suitable to distinguish the species. About the spathula

sternalis, the characteristic chitinized structure on the ventral side of the third instar, more information can be found in the literature. Some variation is apparent. Kieffer (1913b) described a wide structure: "spatule sessile, large, partie basale presque transversale, partie antérieure moins large et bilobée". Rübsaamen & Hedicke (1925—39) depicted a small and oblong one. Möhn (1955) depicted a large and wide spathula. The description, given by Rübsaamen (1891), is remarkable. He described a small, short, bilobed structure, "an dieser Platte scheinen sich zwischen den beiden Lappen noch einige Zähnchen zu befinden". These small teeth were never reported again until Skuhravá & Skuhravý (1960) depicted the spathula. They noted that this particular form of spathula only will be found on larvae (Itonidae sp. in their terminology) living in galls that are coalescent with the spindle of the fruit catkin. They also depicted the two spathula types of *Semudobia* larvae living in fruit galls (in the strict sense), but supposed these to be examples of intraspecific variation.

A short note on phenology. — Many authors indicated the end of March until the beginning of May as the time of emergence of the adults. Forsius (1927), who reported *Semudobia* from Finland, reared adults in August (probably under unnatural conditions, as there are no receptive catkins at that time). This will be discussed below (vide Phenology, pag. 180).

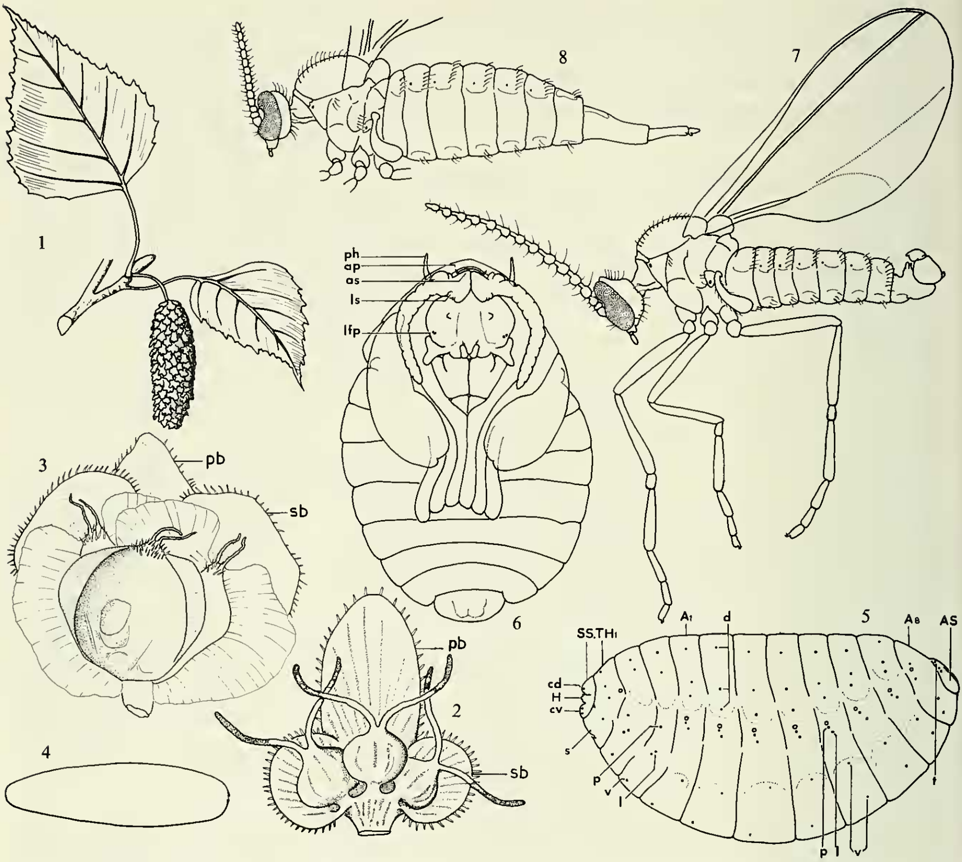
Other references of *Semudobia.* — Macquart (1853), Walker (1856), Döbner (1858), Schiner (1864), Von Bergenstamm & Löw (1876), Inchbald (1885), Lintner (1887), Liebel (1889), Rübsaamen (1892), Von Tubeuf (1893), Collin (1904), Houard (1908—13), Felt (1908, 1915, 1940), Küster (1911), Ross & Hedicke (1927), Docters van Leeuwen (1957), Gäbler (1958), Buhr (1964), Mamaev & Krivosheina (1965), Skuhravá & Skuhravý (1963), Bachmaier (1965), Gagné (1967).

Conclusion. — Differences in gall form (Rübsaamen & Hedicke, 1925—39) and the larval spathula (Skuhravá & Skuhravý, 1960, 1963) have already been recorded. These differences do not represent a range of intraspecific variation. After a careful analysis of material from all over the northern hemisphere, these differences are found to be supported by other characters concerning egg size, papillary pattern in larval and pupal stages, number and form of antennal segments, structure of genitalia and host parasite relations. Thus, it may be concluded that they are differential characters, on which the genus *Semudobia* may be divided into five species.

## Morphology

The gall (fig. 3).

Inflorescences of birches (*Betula,* Betulaceae) are monoecious. The female birch catkin (fig. 1) consists of an elongated spindle bearing spirally arranged condensed dichasia (Porter, 1967). In each dichasium a leaf-like scale bears three axillary female flowers; the fruits are winged nutlets. In this paper, for convenience' sake, the scale is called "bract". This is not quite correct, because in the morphological sense it is a combination of a primary and two secondary bracts (fig. 2). Galling of tissues in the female catkin is exclusively the result of *Semudobia*




Figs. 1—8. Life cycle of *Semudobia.* 1, fruit catkin of *Betula*; 2, scale with female flowers; 3, scale with fruits, the middle one infected; 4, egg; 5, larva; 6, pupa; 7, male; 8, female. A1—A8, abdominal segments; AS, anal segment; H, head; SS, supernumerary segment; TH1, first thoracic segment; ap, apical papilla; as, apical spine; cd, dorsal collar papilla; cv, ventral collar papilla; d, dorsal papilla; l, lateral papilla; lfp, lateral facial papilla; ls, lateral spine; p, pleural papilla; pb, primary bract; ph, prothoracic horn; s, sternal papilla; sb, secondary bract; t, terminal papilla; v, ventral papilla. 3, × 7; 4, × 100; 5,6, × 35; 7,8, × 25. 1,2, after Strassburger et al., 1971.

activities. *Semudobia* galls are never observed outside female birch catkins. Galls may be found when infected catkins are sifted out by separating bracts and nutlets.

Eggs are deposited between the bracts and flowers. Gall forming is induced by the newly hatched larvae, which select the tissue to be infected. The different species prefer different tissues and this results in different gall forms. Detailed information about these forms will be given in the descriptions of the species.

As a rule, only one individual infects one bract or one ovary. Sometimes however, several (up to five!) individuals, which may belong to different species, are found in one single fruitlet. When not attacked by other insects, all these larvae will develop into normal adults. About at the beginning of the second instar a characteristic window-like spot (fig. 97) in the galled fruit is formed by

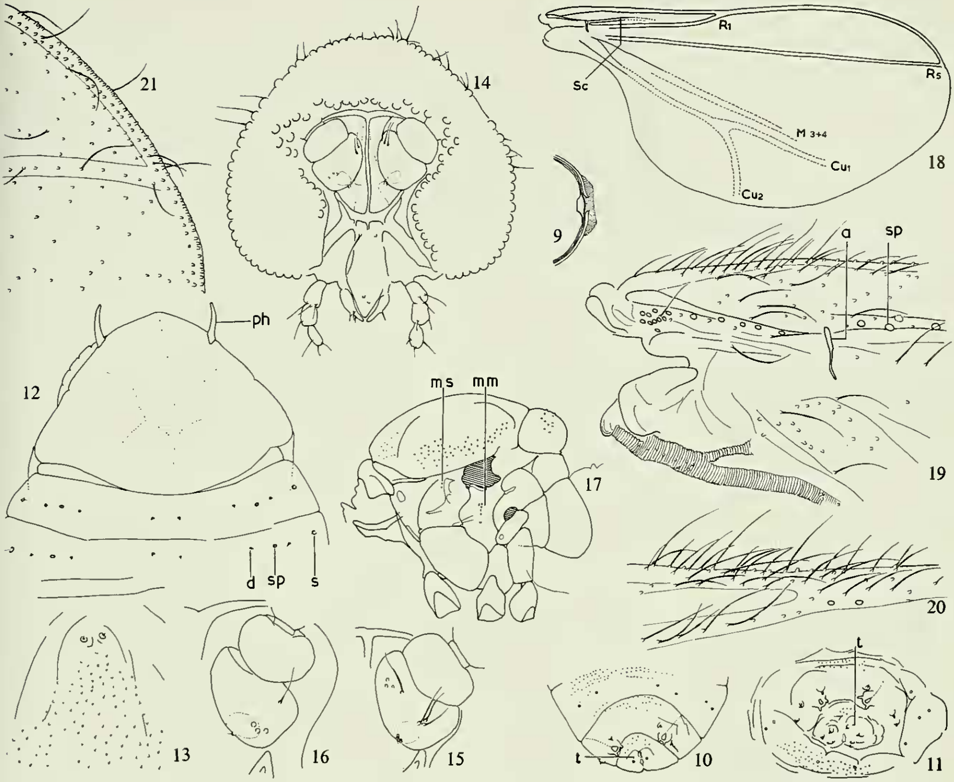



Fig. 9. Egg of *S. tarda*, detail of micropyle; 10—11, anal segment of first instar larva: 10, *S. betulae*, 11, *S. skuhravae*; 12—13, pupa of *S. skuhravae*: 12, dorsal aspect of thorax, 13, anterior ventral papillae on 7th abdominal segment; 14, *S. betulae*, ♂, head; 15—16, ♂, antennal scape: 15, *S. betulae*, 16, *S. brevipalpis*; 17, thorax of *S. betulae*, ♂, lateral aspect; 18—21, wing of *S. betulae*, ♂; 18, venation, 19, detail of base, 20, sensory-pores on distal part of R1, 21, detail of tip. a, arculus; d, dorsal papilla; mm, mesanepimeron; ms, mesanepisternum; ph, prothoracic horn; s, stigma; sp, sensory-pore; t, terminal papilla. 9—11, × 325; 12, × 40; 13, × 250; 14, × 105; 15—16, 19—21, × 165; 17—18, × 35.

some of the species. This window functions as a "weak spot", through which the adults emerge. Some authors (Kieffer, 1895; Pitcher, 1957 and Hodges, 1969) supposed the window to be made by the larval spathula. This can not be correct in this case, because the spathula is only present in the third instar larva.

The egg (fig. 4).

Eggs may be found in the flowering female catkins of birch; they are scattered between the bracts and flowers. For detailed information about oviposition, see Hodges (1969). Freshly laid eggs are transparent, becoming orange-reddish when the larva develops. *Semudobia* eggs are centrolecital, the chorion is smooth and one micropyle is visible on the side where in the ripe egg the anal segment of the embryo will be situated (fig. 9). Egg sizes are taken of ovarian eggs and statistically more or less different egg sizes are found for the individual species (fig. 22). Per

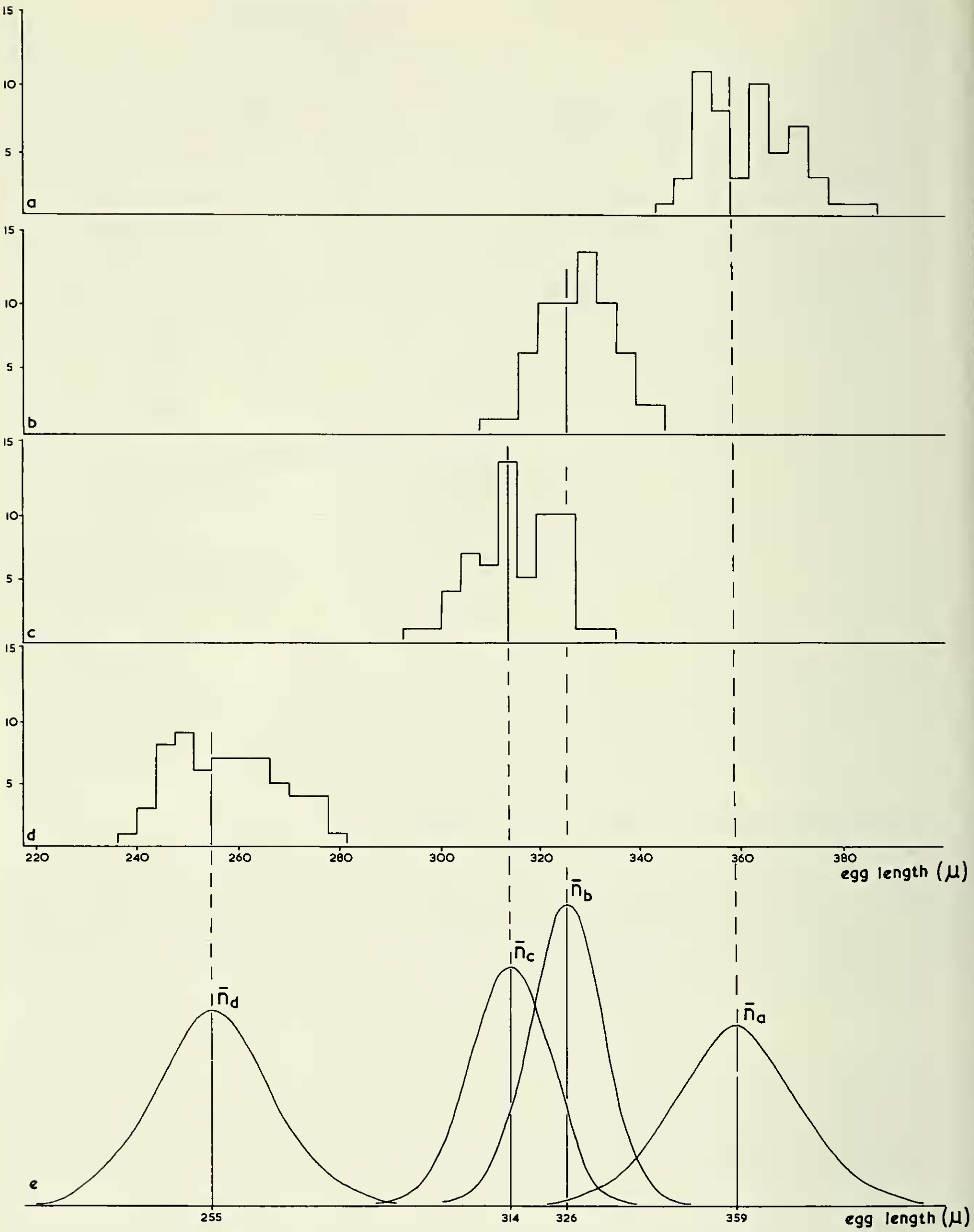



Fig. 22. Egg lengths of *Semudobia*. a—d, histograms: a, *S. skuhravae*, b, *S. betulae*, c, *S. brevipalpis*, d, *S. tarda*; e, corresponding frequency distributions. n̄a, mean value of *S. skuhravae*, n̄b of *S. betulae*, n̄c of *S. brevipalpis*, n̄d of *S. tarda* (*S. steenisi* not studied).

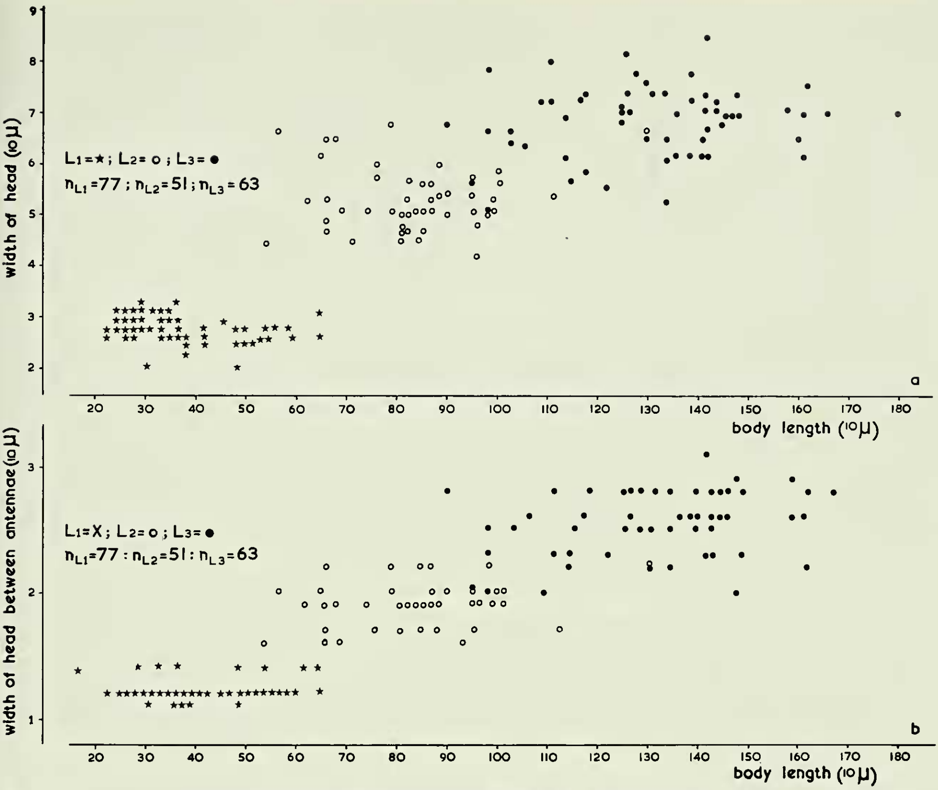



Fig. 23. The relation between body length and width of head (a), respectively width of head between antennae (b) for each of the three larval instars of *S. betulae*.

female five eggs are measured; four females are taken per population and three populations per species.

The larva (fig. 5).

Characters of all larval stages are of great value in gall midge systematics on the generic level. Moreover, they prove to be essential for the delimitation of the species of *Semudobia. Semudobia* midges pass through three larval stages. In all instars the larva consists of a weakly sclerotized head (H), a supernumerary segment (SS), three thoracic segments (Th 1—3) and nine abdominal segments, the last of which is the anal one (A 1—8, AS). From the dorsal side of the head-capsule arises a pair of short antennae. On the ventral side of the antennae a small, oval area is visible. The length of the antenna does not differ remarkably among the different species; it is 2 μ in the first instar, 6 μ in the second and 11 μ in the third. Eye-spots are distinct in all stages, but not in the last inactive period of the third instar in which diapausis is passed. In this full-grown larva the head is retracted into the supernumerary segment. Measurements of the head-capsule are given in the descriptions. As demonstrated in fig. 23, there is no correlation

between length and width of the capsule in any instar. An interstadial growth (as was found by Den Hollander, 1975, for *Tipula*) does not occur in larvae of these midges. *Semudobia* larvae are apodous. The colour of the first instar larva is pale orange, with a bright red spot where the mid gut is situated. There are 9—10 pairs of caeca. The second instar larva is yellowish pale orange and the third instar bright orange; when full-grown, it has a reddish tinged thorax.

Respiration in the first instar is, depending on the species, apneustic or metapneustic; when stigmata are developed, they are situated on A 8. In second and third instar larvae respiration is peripneustic; nine pairs of stigmata are developed on Th 1 and A 1—8.

Papillae are developed in a very definite pattern, that is the same for all instars but different for the various species. The terminology of Möhn (1955) is followed. Papillae are very distinct in the first larval stage. In that stage, only the dorsal, pleural and lateral papillae of A 8 and the terminal papillae of AS have a short seta (up to 1 μ). In the second and third instars, however, usually all papillae have a short seta (— 2 μ). The papillary pattern of the head appears to be very complex and is not dealt with in this study. Depending on the species, the supernumerary segment may bear one pair of dorsal collar papillae (CD) and/or one or two pairs of ventral collar papillae (CV). On the dorsal surface of the thoracic segments, one or two pairs of rows of dorsal papillae (D) are developed, laterally there are two pairs of rows of pleural (P) and one or two pairs of rows of lateral papillae (L, subventral in position). On the ventral surface of Th 1 one pair of sternal papillae (S) is always distinct. The segments Th 2, 3 possess one pair of ventral papillae (V).

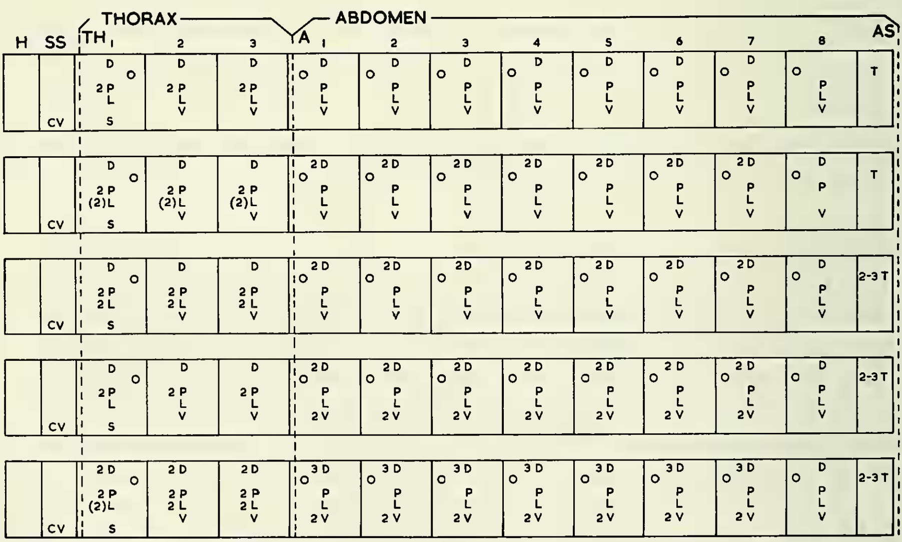



Fig. 24. Diagram of papillary pattern and tracheal system of third instar larvae, lateral aspect. a, *S. tarda*; *S. betulae*; c, *S. brevipalpis*; d, *S. steenisi*; e, *S. skuhravae*. A1—8, abdominal segments; AS, anal segment; CD, dorsal collar papilla; CV, ventral collar papilla; D, dorsal papilla; H, head; L, lateral papilla; P, pleural papilla; S, sternal papilla; SS, supernumerary segment; T, terminal papilla; THl—3, thoracic segments; V, ventral papilla; O, stigma.

The dorsal surface of the abdominal segments A 1—7 offers the best diagnostic characters in papillary pattern. Depending on the species, 1—3 pairs of rows of dorsal papillae may be developed. Laterally one pair of rows of pleural papillae and one pair of rows of laterals can be observed. On the ventral surface of the segments A 1—7 there may be one pair of anterior papillae and/or one pair of posterior papillae. The anterior ventral papillae are in most species only visible in the young first instar. The A 8 segment has a more simple pattern. One pair of dorsal papillae is present in all species except one, in another species there are usually no lateral papillae. In general, one pair of both pleural and ventral papillae are present. Depending on the species, 1—3 pairs of papillae are present on the anal segment. In second and third instar larvae papillae are situated outside the anal field (a distinct area around the anus); these may be distinguished as terminal papillae (t, fig. 85). In the first instar larva, where the delimitation of the anal field is not clear (fig. 10, 11), the discrimination between anal and terminal papillae may be a moot point. Contrary to Möhn (1955), Hodges (1969) considered a papilla a simple skin-structure and not a sense-organ. The statements by Kieffer (1895) and Möhn (1955) that pleural papillae are not developed in *Semudobia* must be imputed to the less sophisticated microscopy techniques of that time. Papillary patterns are scheduled in fig. 24.

Skin structures, such as well developed spinule rows, are visible on the ventral and dorsal surfaces of the first instar larvae. On the dorsal surface of second instar larvae spinule rows may be less distinct. In regard to spinule rows it is possible to divide larval segments in an anterior and a posterior part. In the anterior part, the spinule rows are always distinct and they lie close to each other; in the posterior part, however, they lie further apart or, more often, are absent. The spinule rows are counted and the numbers are given in the descriptions. The first number concerns the posterior part of Th 3, the second relates to the anterior part of A 1. Between brackets the variation in number is given usually for ten specimens. Skin structures and papillae are distinct in newly hatched first instar or just moulted second instar larvae, but they become less distinct in older first and second stages. The third instar larva has a verrucose surface. Dorsally there are no remarkable differentiations, but ventrally the verrucae unite to form striae, while laterally they tend to be isolated and more rounded. In the figs. 72, 73, e.g., small fields are indicated that have no verrucose sculpture. On the ventral surface of the third instar prothorax (Th 1) lies a heavily chitinized structure: the spathula sternalis. Shape and size of the spathula, as suggested earlier, give good characters for the delimitation of the species.

When full-grown (about mid August, in The Netherlands), the larva produces a whitish membraneous cocoon (see also Hodges, 1969) and is ready to hibernate.

The pupa (fig. 6).

In morphology and descriptions of the pupal stage mainly Möhn (1961) is followed. The colour of the pupa is bright orange. On the head, near the place where the adult pedicel will develop, two heavily chitinized blunt apical spines are formed. These spines help the pupa to perforate the window-pit of the gall just

before the adult emerges. Next to the apical spines two subrotund laterals are visible. Frontal spines are absent, on the ventro-lateral part of the future adult eye, one or two pairs of papillae are situated. Just caudal of the apical spines, a pair of slender apical papillae is present. From the dorsal side of the prothorax a pair of stout prothoracic horns (fig. 12) arises, on the end of which the prothoracic stigmata are located. The papillary pattern on the abdominal segments A 1—8 is in conformance with those of the larval stages and here also offer the best diagnostic characters. In the pupa, the anterior ventral papillae are often distinct (fig. 13). On the dorsal surface of A 1—7 a pair of rows of sensory-pores is also formed (fig. 12). The abdomen is covered with tiny, pointed setulae (fig. 13).

The adult.

In the descriptions of the adult stage mainly Harris (1966, 1968) is followed. For further details, see Gagné (1968, 1973) and Yukawa (1971), from whom some of the terms used are borrowed.

Male (fig. 7). — Body reddish-orange, with dark brown sclerotized parts. Eyes holoptic (fig. 14), with a slight, incomplete, median incision. Antenna with scape, pedicel and, depending on the species, 12—14 flagellomeres. The distal flagellomeres are often fused. If the last flagellomere is more than 1½ times the length of the penultimate one, the total count of flagellomeres is given as "$n^+$" in the descriptions, rather than "n". Flagellomeres uninodal with subquadrate internodes (stalks); sensorial spines present, usually two per flagellomere and situated on antero-distal portion (fig. 33); circumfila simple, not looped; basal setae on horseshoe-shaped sockets. Scape larger than pedicel, with a ventral area with very short setae and laterally and distally fields with long setae (fig. 15). Maxillary palpi three segmented.

Numbers of setae on mesanepisternum and mesanepimeron (fig. 17) are given in the descriptions. Sc of wing usually incomplete or absent, and indicated only by a number of sensory-pores (fig. 19); R5 well separated from R1, and joining C near wing apex. Cu halfway forked in Cu1 and Cu2; m 3 + 4, Cu1 and Cu2 only indicated as wing-folds; Rs absent. Tarsal claws simple, bent nearly at right-angle and a little shorter than empodia.

Abdominal terga 2—7 not strongly sclerotized, caudal row of setae present, basal row absent, only one pair of short setae cephalad of caudal row; sterna 2—7 with both basal and caudal rows of setae, one pair of median short setae cephalad of the basal row. Basimere (fig. 46) of genitalia stout with in internal angle a large claspette (mesolobe); distimere stout, in some species a little inflated, about half as long as basimere and with a dense row of strong teeth distally; superior lamella (tergum 10) with V-shaped incision, forming a pair of lobes which are rounded distally; inferior lamella (sternum 10) narrower than superior lamella and, depending on the species, shallowly emarginated to with V-shaped incision; aedeagus rather thick, distinctly shorter to a little longer than claspette.

Female (fig. 8). — Antenna with scape, pedicel and 11—13 subsessile flagellomeres. Ovipositor retractile, tapering to a simple upper lamella and a short to very short lower lamella (fig. 56, 57).

## METHODS

Measurements of galls are taken in dry condition; in the case of fruit galls stigmata and wings are excluded. Sizes of galls given are only valid for the host plant species mentioned in the descriptions and for the galls inhabited by one gall midge only.

Eggs are dissected from identified females and macerated in warm (85-90°C) 80% lactic acid. After being straightened under a cover-slip, length and width are measured in the same medium. Midges, from which ovarian eggs are taken, are preserved on a 70 : 15 : 15% aethanol-glycerol-water mixture. Eggs of females preserved in other ways may not give comparable results.

Preparation of the larvae, especially of first and second stages, may cause many difficulties. Therefore rather detailed information is given here about techniques. Newly hatched larvae are collected from catkins just after flowering. These catkins are freshly deep-frozen or preserved on a 70 : 15 : 15% mixture of aethanol-glycerol-water. Older larvae are dissected from fresh or dried (herbarium specimens) galls and preserved either dry, or in the same aethanol-glycerol-water mixture. Fresh larvae are macerated in warm 80% lactic acid. Larvae from dried galls first have to be hydrated carefully in a series of 90, 70, 30% solutions of aethanol and in water before maceration in 80% lactic acid is possible. Swelling of the body content, which might result in total distortion of the larval skin, is thus prevented. Small larvae, first instar and young second instar, are examined in the maceration medium. For a slide collection these larvae are mounted in polyvinyl-lactophenol (Chroma Gesellschaft Schmid & Co., Stuttgart, Germany). To avoid shrinking, the very tender skins are transferred to the mounting medium without neutralizing or rinsing. The older larvae are washed in water after maceration and the residuals of body contents are very carefully removed. The macerated larvae are stored and examined in glycerol.

Pupae are dissected from the galls and macerated in 80% lactic acid. After rinsing the pupae have to pass a series of 30, 70, 96% aethanol before being mounted in euparal.

Measurements of all immature stages are taken from specimens straightened under a cover-slip.

To rear the adults, galls are sorted according to the identification key for the galls on page 166. The samples, mixed with peat-litter and deposited in glass-vials, are allowed to pass diapause under more or less natural conditions. From January on, the glass vials are transmitted to sand-filled flowerpots and kept in a climate chamber (20° C, long day light regime). The cultures are moistened with 1% propionic acid to prevent damage by mould infections. After emergence the adults are promptly killed in a mixture of 70 : 15 : 15% aethanol-glycerol-water and stored in the same medium. Because maceration might disturb tiny organs as antennae, the specimens are directly dehydrated in a series of 30, 70, 96% aethanol. After clearing in oil of cloves the specimens are mounted in euparal. On the slide the head, left wing and male genitalia are mounted under separate cover-slips. The body is slide-mounted in a lateral position, the head with the face up, the genitalia dorsal surface up.

For examination a phase-contrast microscope (Zeiss, objectives Ph 10, 25, 40 and 63 ×) is used.

## TAXONOMIC PART

### **Semudobia** Kieffer

*Cecidomyia* Meigen (partim); Winnertz, 1853: 234.
*Hormomyia* Rübsaamen, 1891: 137.
*Oligotrophus* Latreille (partim); Kieffer, 1900: 22.
*Semudobia* Kieffer, 1913a: 55.

Type-species: *Cecidomyia betulae* Winnertz, 1853:234.

### Keys to species of *Semudobia*

(Egg sizes are not used in the keys because their accurate analysis was only performed in the ovarian stage; fig. 22.)

#### Males

1. Third palp segment shorter than the second; claspettes rectangular, distally emarginated; mainly Palaearctic species . . . . . . . . . . . . . . . *tarda* sp. n.
— Third palp segment longer than the second; claspettes more or less triangular, never distally emarginated . . . . . . . . . . . . . . . . . . . . . . . . . . 2
2. Ultimate flagellomere rather rounded, internodes transverse to subquadrate; first and second palpal segments not broadly fused; claspettes verrucose; aedeagus usually a little shorter than claspettes . . . . . . . . *skuhravae* sp. n.
— Ultimate flagellomere rather pointed, internodes oblong; first and second palpal segment broadly fused; surface of claspettes only finely sculptured; aedeagus always a little longer than claspettes . . . . . . . . . . . . . . . . . 3
3. Antenna with 14 flagellomeres, at least 3 times the width of the head; internode of third flagellomere at least 0.5 times the length of the node of this segment; West-Nearctic species . . . . . . . . . . . . . . . . . . *steenisi* sp. n.
— Number of flagellomeres less than 14, length of antenna never more than 2.6 times the width of the head . . . . . . . . . . . . . . . . . . . . . . . . . . 4
4. Never more than one seta on distal surface of scape and then laterally placed (fig. 16); third palpal segment at least 1.7 times the length of the second; at least 5 setae on mesanepisternum and 8 on mesanepimeron; inferior lamella about half-way with U-shaped incision, lobes acute; East-Nearctic species . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . *brevipalpis* sp. n.
— 3—10 setae on distal surface of scape (fig. 15); length of third palpal segment not more than 1.4 times the length of the second; not more than 3 setae on mesanepisternum and not more than 5 on mesanepimeron; inferior lamella not more than for about one-third V-shapedly incised, lobes rounded; mainly Palaearctic species . . . . . . . . . . . . . . . . . . . . . . . . . . *betulae* Wtz.

## Females

1. Tergum 8 triangular, length of this sclerite about equal to its width; ovipositor always longer than hind femur, with heavily chitinized vaginal furca; inferior lamella very short and truncate; mainly Palaearctic species . . . *tarda* sp. n.
— Tergum 8 sub-triangular or rectangular to H-shaped, always somewhat longer than wide; ovipositor shorter than hind femur; vaginal furca not remarkably chitinized; inferior lamella at least a little shorter than wide, rounded . . . 2
2. Ultimate flagellomere rounded; first and second palpal segments never broadly fused . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . *skuhravae* sp. n.
— Ultimate flagellomere pointed; first and second palpal segments broadly fused . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . 3
3. Antenna at least two times the width of the head; West-Nearctic species . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . *steenisi* sp. n.
— Antenna never more than two times the width of the head . . . . . . . . . . 4
4. Distal setae on scape, when present, then placed laterally; third palpal segment at least 1.5 times the length of the second, length of tergum 8 never more than 1.5 times its width; length of superior lamella about 1.3 times its height; East-Nearctic species . . . . . . . . . . . . . . . . . . . . . . . . . . . *brevipalpis* sp. n.
— Distal setae on scape, when present, never placed laterally; third palpal segment never more than 1.5 times the length of the second; length of tergum 8 about two times its width; length of superior lamella at least two times its height; mainly Palaearctic species . . . . . . . . . . . . . . . . . . *betulae* Wtz.

## First instar larvae[1])

(No stigmata, or only one pair of stigmata developed, spathula sternalis absent.)

1. No stigmata developed at all; only one pair of rows of dorsal papillae on abdominal segments A 1—7, no dorsal papillae on A 8 (the penultimate body segment) . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . *tarda* sp. n.
— One pair of stigmata on A 8; at least two pairs of rows of dorsal papillae on segments A 1—7, one pair on A 8 . . . . . . . . . . . . . . . . . . . . . . . . . 2
2. Three pairs of rows of dorsal papillae on A 1—7, one pair of dorsal collar papillae, on A 8 pleural and lateral papillae both developed *skuhravae* sp. n.
— Two pairs of rows of dorsal papillae on A 1—7, no dorsal collar papillae, on A 8 no lateral papillae developed . . . . . . . . . . . . . . . . . . . . . *betulae* Wtz.

## Second instar larvae

(Stigmata developed on first thoracic segment and first to eighth abdominal segments; no spathula sternalis. Same key as for third instar, characters based on spathula excluded.)

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[1]) Nearctic species not studied and therefore excluded from this key.

### Third instar larvae

(Nine pairs of stigmata (vide second instar) and spathula sternalis developed.)

1. Spathula sternalis with a variable number of smaller teeth (as if broken off) between the usually larger lobes; three pairs of rows of dorsal papillae on A 1—7 . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . *skuhravae* sp. n.

— Spathula always bilobed; only one or two pairs of rows of dorsal papillae on A 1—7 . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . 2

2. Spathula large, lobes at least 15 μ high; only one pair of rows of dorsal papillae on A 1—7 . . . . . . . . . . . . . . . . . . . . . . . . . . . . . *tarda* sp. n.

— Spathula smaller, height of lobes never more than 10 μ; always two pairs of rows of dorsal papillae . . . . . . . . . . . . . . . . . . . . . . . . . . . 3

3. Spathula oblong, at least 50 μ high; no lateral papillae on A 8, only one pair of terminal papillae; mainly Palaearctic species . . . . . . . . . . . *betulae* Wtz.

— Spathula subquadrate to transverse, never more than 50 μ high; lateral papillae on A 8 present, 2—3 pairs of terminal papillae . . . . . . . . . . . . . . . . . 4

4. Lobes of spathula at least 5 μ high, one pair of rows of lateral papillae on thoracic segments, two pairs of rows of ventrals on segments A 1—7; West-Nearctic species . . . . . . . . . . . . . . . . . . . . . . . . . *steenisi* sp. n.

— Lobes of spathula never more than 5 μ high, two pairs of rows of lateral papillae on thoracic segments, one pair of rows of ventrals on segments A 1—7; East-Nearctic species . . . . . . . . . . . . . . . . . . . *brevipalpis* sp. n.

### Pupae[1])

1. Two pairs of rows of dorsal papillae, dorsally of sensory-pores, on abdominal segments A 1—7 . . . . . . . . . . . . . . . . . . . . . . . . *skuhravae* sp. n.

— Only one pair of rows of dorsal papillae, dorsally of sensory-pores, on A 1—7 . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . 2

2. No dorsal papillae laterally of sensory-pores on A 1—7, dorsal papillae on A 8 absent . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . *tarda* sp. n.

— One row of dorsal papillae laterally of sensory-pores on A 1—7, one pair of dorsal papillae on A 8 . . . . . . . . . . . . . . . . . . . . . . . . . . . . 3

3. Prothoracic horn longer than 120 μ, about 0.08 times the body-length or more; mainly Palaearctic species . . . . . . . . . . . . . . . . . . . . . . *betulae* Wtz.

— Prothoracic horn shorter than 100 μ, about 0.06 times the body-length or less; West-Nearctic species . . . . . . . . . . . . . . . . . . . . . . . . *steenisi* sp. n.

### Galls

1. Either the axil of the scale is galled, or the galled fruit is distinctly coalescent with the scale; window-pit absent . . . . . . . . . . . . . . . . . *skuhravae* sp. n.

— Galling of the fruit, the gall is in ripe situation never coalescent with the scale . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . 2

2. Window-pit absent or indistinct, gall subrotund and glabrous, wings of fruit often completely reduced . . . . . . . . . . . . . . . . . . . . . . . . *tarda* sp. n.

[1]) *S. brevipalpis* not studied and therefore excluded from this key.

— Window-pit(s) distinct . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . 3
3. Often a window-pit on both sides of the gall, one of them large; gall glabrous, wings of fruit often completely reduced; East-Nearctic species *brevipalpis* sp. n.
— Only one window-pit developed; gall more or less hairy, wings present . . 4
4. Gall usually concave on ad-axial side, window-pit irregularely formed; West-Nearctic species . . . . . . . . . . . . . . . . . . . . . . . . . . . . *steenisi* sp. n.
— Gall usually convex on both sides, window-pit subrotund; mainly Palaearctic species . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . *betulae* Wtz.

## **Semudobia betulae** (Winnertz)

(male: figs. 14, 15, 17—21, 32, 33, 42, 43; female: figs. 40, 41, 50, 54, 55, 102; imm. stages: figs. 10, 64, 65, 70—75, 95—97)

Male. — Width of head 1.17 (1.12—1.30) times its height. Antenna (figs. 32, 33) with 2 + 12 segments, its length 2.53 (2.49—2.60) times the width of head; scape ventrally with 2 (2—4) very short, 4 (3—4) lateral and 10 (3—10) dorsal long setae; third flagellomere with its node 1.07 (1.00—1.08) times as long as its diameter; internodes oblong, internode of third flagellomere 0.48 (0.38—0.48) times as long as node. Maxillary palp 0.24 (0.24—0.28) times the width of head; third segment 1.27 (1.14—1.38) times as long as the second; first and second segments partially grown together. Fronto-clypeal setae 7 (2—7); 2 (2—3) setae on mesanepisternum, 5 (4—6) on mesanepimeron. Wing length 1.68 (1.56—1.74) mm, 2.0 (1.9—2.2) times as long as wide; R5 2.3 (2.2—2.3) times as long as R1; Sc indicated by 4 (3—4) sensory-pores, 4 (3—5) sensory-pores on basal part of R1 and 2 on distal part, 3 pores on medio-distal portion of R5. Tibia of hind leg 0.94 (0.78—0.98) times as long as femur, second tarsal segment 0.54 (0.46—0.57) times this length; fifth tarsal segment 0.85 (0.83—0.85) times as long as the fourth. Distimere (fig. 42) 0.47 (0.47—0.58) times as long as basimere; inferior lamella weakly emarginate to incised for about one-third, the incision broadly V-shaped, its sides converging to its apex (fig. 43); aedeagus a little longer than the usually weakly chitinized, rounded triangular claspettes.

Female. — Width of head 1.15 (1.15—1.28) times its height. Antenna (figs. 40, 41) with 2 + $11^{+}$ ($10^{+}$—12) segments, its length 2.00 (1.44—2.00) times the width of head; scape ventrally with 3 (2—3) very short, 3 (2—3) lateral and 3 (0—3) dorsal long setae; third flagellomere with its node 1.08 (1.04—1.09) times as long as its diameter. Maxillary palp (fig. 102) 0.28 (0.24—0.30) times the width of the head; length of third segment 1.46 (1.25—1.46) times the length of the second; first and second segments partially grown together. Fronto-clypeal setae 10 (1—10); 3 (2—3) setae on mesanepisternum, 7 (5—7) setae on mesanepimeron. Wing length 2.00 (1.66—2.14) mm, 2.1 (2.0—2.1) times as long as wide; R5 2.4 (2.3—2.4) times as long as R1; Sc indicated by 5 sensory-pores, 6 (4—6) sensory-pores on basal part of R1 and 2 on distal part, 3 on medio-distal portion of R5. Tibia of hind leg 0.89 (0.88—0.90) times as long as femur, second tarsal segment 0.43 (0.41—0.46) times this length; fifth tarsal segment 0.86 (0.83—0.92) times as long as the fourth. Tergum 8 subtriangular (fig. 50), the height of this sclerite about 2 times its width. Ovipositor (fig. 55) 0.75 (0.75—0.87) times as long as hind femur, for one- to about

three-quarters retracted into the eighth abdominal segment; vaginal furca not remarkably chitinized; superior lamella 2.5 (2.3—3.0) times as long as high; inferior lamella with a length about equal to its width (fig. 54).

Immature stages. — Egg length $\bar{n}$ 326 μ, $\bar{n}$ ± 2 SD. (95% of egg lengths) between 312—340 μ; width $\bar{n}$ 106 μ. First instar larva (figs. 64, 65); length 255 (221—642), width 73 (73—339) μ; width of head-capsule 26 (21—47) μ, between antennae 12 (11—14) μ, n = 76; dorsal spinule-rows 4 (4—0) + 9 (7—10), ventrals 4 (4—0) + 8 (7—9), n = 10; respiration metapneustic. Second instar (fig. 70); length 664 (537—1296), width 269 (269—664) μ; width of head-capsule 65 (45—68), between antennae 22 (16—22) μ, n = 50; dorsal spinule-rows in posterior part absent, in anterior 4 (4—0), ventrals in posterior part absent either, in anterior part 8 (8—0), n = 10. Third instar (figs. 71—73); length 1422 (901—1801), width 948 (584—1138) μ; width of head-capsule 71 (45—85), between antennae 23 (17—31) μ, n = 63; spathula sternalis bilobed (figs. 74, 75), width 24 (19—28), height 60 (52—64), distance between points of lobes 14 (13—22), height of lobes 9 (8—9), height of median incision 9 (5—9) μ, n = 10. Pupa length 1228 (1212—1643), prothoracic horns 126 (122—146), apical papillae 28 (28—43) μ, n = 8; sensory-pores between the corresponding papillae of the two pairs of dorsal rows (fig. 95).

Papillary pattern (fig. 24b). Dorsal collar papillae absent, one pair of ventral collar papillae. On thoracic segments one pair of dorsal papillae, 2 pairs of pleural papillae and (one or) two pairs of laterals; on Th 1 one pair of sternal papillae, on Th 2 and 3 one pair of ventrals. On segments A 1—7 two pairs of dorsal papillae, one pair of pleurals and one pair of laterals, one (or two) pairs (posterior ventral papillae only distinct in first instar) of ventral papillae; on A 8 one pair of dorsal, pleural and ventral papillae, lateral papillae absent; one pair of terminal papillae on AS.

Gall (fig. 97) length 1.6—2.1 mm, $\bar{n}$ 1.8 mm, width 1.0—1.8 mm, $\bar{n}$ 1.3 mm, n = 20; galling of the fruit; gall ovoid, more or less hairy, wings present, although not so large as in healthy fruits; window-pit distinct (*B. pubescens*).

Type material. — The type of *Cecidomyia betulae* Winnertz was destroyed in 1945 during the bombing of the Zoological Museum of Bonn (Möhn and Ulrich, in litt.), and no other specimens of the original series exist. In regard to the (wrong) low number of antennal segments in the original description, there is a good chance that the type-specimen Winnertz described, belonged to this species. The other species that could have been in Winnertz' material, all have more antennal segments. Moreover, in Poland, where the type-locality is situated, this species seems to be most common. A new type is selected: Neotype ♂, slide no. 760223.8, The Netherlands, Renkum, 15.i.1975, ex fruit galls of *B. pendula*, Allotype ♀, slide no. 760206.3, The Netherlands, Meyendel, 28.iv.1975, ex fruit galls of *B. pubescens*, leg. J. C. Roskam. Although this material does not originate from Poland, it comes as near to the original type locality as in my case is practicable (cf. Code, article 75 c5).

The original host-plant, *B. alba*, is a polytypic species, comprising among others *B. pendula* and *B. pubescens*. Paratypical material is presented to the Bonn Museum.

Material (all my localities are from The Netherlands) in coll. Rijksmuseum van Natuurlijke Historie, Leiden. Adults slides no. 760223.7—8, 760206.2—3, 760216.1, Renkum, 15.i.1975, ex fruit galls of *B. pendula* (♂); Meyendel, 28.iv.1975, ex fruit galls of *B. pubescens* (♀). First instar larva slide no. 750519.1, Duivenvoorde, 19.v.1975, ex *B. pubescens;* second instar slide no. 750619.4, Duivenvoorde, 19.vi.1975, ex fruit galls of *B. pubescens;* third instar slide no. 751001.1, Meyendel 1.x.1975, ex fruit galls of *B. pubescens;* pupa slides no. 730402.1—2, 730410.1—4, Meyendel, 2 and 10.iv.1973, ex fruit galls of *B. pendula,* leg. J. C. Roskam.

## **Semudobia brevipalpis** sp. nov.

(male: figs. 16, 30, 31, 44, 45; female: figs. 38, 39, 51, 56, 57, 103; imm. stages: figs. 77—81, 98)

Male. — Width of head 1.32 (1.25—1.32) times its height. Antenna (figs. 30, 31) with 2 + $13^+$ ($12^+$—$13^+$) segments, its length 2.45 (2.41—2.60) times the width of the head; scape ventrally with 1 (0—1) very short, 5 (4—5) lateral and 1 (0—1) latero-distal long setae; third flagellomere with its node 1.10 (1.04—1.15) times as long as its diameter; internodes oblong, internode of third flagellomere 0.42 (0.42—0.48) times as long as the node. Maxillary palp 0.19 (0.19—0.22) times the width of head; third segment 2.00 (1.73—2.20) times as long as the second; first and second segments partially grown together. Fronto-clypeal setae 2 (2—5), 12 (5—13) setae on mesanepisternum, 11 (8—11) on mesanepimeron. Wing length 1.78 (1.52—1.78) mm, 2.0 (2.0—2.1) times as long as wide; R5 2.2 (2.1—2.2) times as long as R1; Sc indicated by 4 (4—5) sensory-pores, 4 (4—6) pores on basal part and 3 (2—3) on distal part of R1, 3 sensory-pores on medio-distal portion of R5. Tibia of hind leg 0.76 (0.72—0.87) times as long femur, second tarsal segment 0.44 (0.43—0.50) times this length; fifth tarsal segment 0.85 (0.80—0.91) times as long as fourth. Distimere acute (fig. 44), 0.55 (0.45—0.56) times as long as basimere; inferior lamella about half way U-shapedly incised, sides converging to apex, lobes distally acute (fig. 45); aedeagus a little longer than the weakly chitinized, broadly rounded triangular claspettes.

Female. — Width of head 1.32 (1.31—1.34) times its height. Antenna (figs. 38, 39) with 2 + $11^+$ (10—12) segments, its length 1.61 (1.56—1.67) times the width of head; scape ventrally with 1 (0—1) very short, 4 (3—4) lateral and 1 (0—1) latero-distal long setae; third flagellomere with its node 1.09 (1.09—1.25) times as long as its diameter. Maxillary palp (fig. 103) 0.19 (0.19—0.24) times the width of head; length of third segment 2.00 (1.55—2.22) times the length of second; first and second segments partially grown together. Fronto-clypeal setae 2 (0—4), 4 (3—6) setae on mesanepisternum, 6 (3—14) setae on mesanepimeron. Wing length 1.68 (1.68—1.84) mm, 2.18 (2.17—2.31) times as long as wide; R5 2.22 (2.10—2.22) times as long as R1; Sc indicated by 4 (3—4) sensory-pores, 3 pores on basal and 2 (2—3) on distal part of R1, 3 on medio-distal portion of R5. Tibia of hind leg 0.83 (0.82—0.87) times as long as femur, second tarsal segment 0.46 (0.44—0.49) times this length; fifth tarsal segment 0.89 (0.82—0.91) times as long as fourth. Tergum 8 triangular (fig. 51), the height of this sclerite a little more than its width. Ovipositor (fig. 57) 0.71 (0.70—0.73) times as long as hind femur, for about the half retracted

into the eighth abdominal segment; vaginal furca not remarkably chitinized, superior lamella about a third longer than high, inferior lamella a little shorter than wide (fig. 56).

Immature stages. — Egg length $\bar{n}$ 314 μ, $\bar{n}$ ± 2 SD (95% of egg lengths) between 297—331 μ; width $\bar{n}$ 112 μ. First, second instar larvae and pupae are not collected. Third instar (figs. 77—79): length 1388 (1101—1404), width 1069 (718—1084) μ, width of head-capsule 79 (61—83), between antennae 24 (20—28) μ; spathula sternalis very wide with two small lobes (figs. 80, 81); width 55 (42—71), height 25 (16—28), distance between points of lobes 39 (28—52), height of lobes 3 (2—5), height of median incision 6 (5—8) μ, n = 15. Pupae not collected.

Papillary pattern (fig. 24c) very similar to *S. betulae*. Lateral papillae present on A 8, on AS 2—3 pairs of terminal papillae.

Gall (fig. 98) length 1.5—2.0 mm, $\bar{n}$ 1.8 mm, width 0.9—1.4 mm, $\bar{n}$ 1.2 mm, n = 20; galling of the fruit, the gall is obovate and glabrous, wings almost completely reduced, window-pit distinct, usually developed on both ad- and abaxial side of the gall *(B. populifolia)*.

Type material. — Holotype ♂, slide no. 760220.4, Allotype ♀, slide no. 760318.1. Canada, Quebec, natural forest along Trans-Canada Highway, 9.ii.1975, ex fruit galls of *B. papyrifera*, leg. W. F. Grant.

Material in coll. Rijksmuseum van Natuurlijke Historie, Leiden. Adults slides no. 760220.1,3—4, 750209.10, 760213.1, 760218.2—3, same data as type material. Third instar larva slide no. 761101.14, same data as type-material.

The species is quite close to *S. betulae:* the larvae and pupae have two pairs of rows of dorsal papillae on the abdomen, also the adult antennae are quite similar. Nevertheless there are striking differences, viz., in the larvae the broad spathula with the very small lobes, in the adults the bristles in latero-distal position on the scape, the very short second palp segment, the broadly emarginated inferior lamella in the male and the short, plump superior lamella in the female genitalia.

## **Semudobia steenisi** sp. nov.

(male: figs. 109, 110, 113, 114; female: figs. 106—108, 111, 112, 115; imm. stages: figs. 116—122)

Male. — Width of head 1.12 (1.09—1.16) times its height. Antenna (figs. 109, 110) with 2 + 14 segments, its length 3.39 (3.18—3.97) times the width of head; scape ventrally with 4 (1—4) very short, 3 (3—4) lateral and no dorsal long setae; third flagellomere with its node 1.00 (1.00—1.06) times as long as its diameter; internodes oblong, internode of third flagellomere 0.63 (0.58—0.65) as long as the node. Maxillary palp 0.24 (0.22—0.28) times the width of head, third segment 1.20 (1.12—1.35) times as long as second; first and second segments partially grown together. Fronto-clypeal setae 2 (2—5); setae on mesanepisternum 1 (0—3), 2 (2—5) setae on mesanepimeron. Wing length 1.86 (1.64—1.91) mm, 2.29 (2.28—2.46) times as long as wide; R5 2.11 (1.88—2.17) times as long as R1; Sc indicated by 6 (4—7) sensory-pores, sensory-pores on basal part of R1 indistinct and 2 on distal part, 3 pores on medio-distal portion of R5. Tibia of hind leg 0.79 (0.76—0.91) times as long as femur and second tarsal segment 0.59 (0.50—0.64) this length; fifth tarsal segment 0.62 (0.62—0.77) times as long as fourth. Distimere

(fig. 113) 0.46 (0.46—0.52) times as long as basimere; inferior lamella weakly emarginate (fig. 114); aedeagus about as long as the chitinized, triangular, rather slender claspettes.

Female. — Width of head 1.15 (1.12—1.15) times its height. Antenna (figs. 111, 112) with 2 + 12+ segments, its length 2.07 (2.03—2.33) times the width of head; scape ventrally with 2 (2—4) very short, 3 lateral and no dorsal long setae; third flagellomere with its node 1.06 (1.00—1.11) times as long as its diameter. Maxillary palp (fig. 115) 0.31 (0.28—0.32) times the width of the head; length of third segment 1.15 (1.06—1.20) times the length of the second; first and second segments partially grown together. Fronto-clypeal setae 3 (2—3); 3 (2—5) setae on mesanepisternum, 3 (2—4) setae on mesanepimeron. Wing length 1.86 (1.84—2.00) mm, 2.48 (2.31—2.48) times as long as wide; R5 2.11 (2.11—2.28) times as long as R1; Sc indicated by 4 (4—7) sensory-pores, 3—5 indistinct sensory-pores on basal part of R1 and 2 (2—3) on distal part, 3 pores on medio-distal portion of R5. Tibia of hind leg 0.79 (0.77—0.82) times as long as femur, second tarsal segment 0.63 (0.61—0.70) times this length; fifth tarsal segment 0.77 (0.77—0.87) times as long as fourth. Tergum 8 bluntly triangular to H-shaped (fig. 108), the height of this sclerite about one-and-a-half times its width. Ovipositor (fig. 106) 0.77 (0.72—0.81) times as long as hind femur, for one to about three-quarters retracted into the eighth abdominal segment; vaginal furca not remarkably chitinized; superior lamella 1.92 (1.71—1.92) times as long as high; inferior lamella a little shorter than wide (fig. 107).

Immature stages. — Egg length and first instar larvae not studied. Second instar (fig. 117) length 821, width 483 μ; width of head-capsule 47, between antennae 17 μ; dorsal spinule rows in posterior part absent, in anterior part 3; ventrals in posterior part absent too, in anterior part 7; n = 1. Third instar (figs. 118—120) length 1563 (1420—1723) μ, width 1101 (909—1196) μ; width of head-capsule 57 (52—86), between antennae 30 (28—39) μ, spathula sternalis (figs. 121, 122) bilobed, it may form one structure or consist of two independent pieces; width 31 (28—52), height 22 (19—42), distance between points of lobes 11 (11—39), height of lobes 6 (5—8), height of median incision 8 (6—9) μ, n = 16. Pupa length 1372 (1324—1627) μ; prothoracic horns 79 (71—94) μ; apical papillae 30 (25—36) μ; n = 4.

Papillary pattern (fig. 24d) rather similar to *S. betulae.* Only one pair of lateral papillae on thoracic segments and two pairs of ventrals on segments A 1—7; on AS 2—3 pairs of terminal papillae.

Gall (fig. 116) length 2.1—3.0 mm, $\bar{n}$ 2.6 mm, width 1.4—2.1 mm, $\bar{n}$ 1.8 mm, n = 20; galling of the fruit; the gall is obovate and usually concave on ad-axial side, more or less hairy, wings present, although not so large as in healthy fruits; window-pit distinct *(B. occidentalis).*

Type material. — Holotype ♂, slide no. 761101.4, Allotype ♀, slide no. 761101.10. U.S.A., Wyoming, Fremont County, Wind River, 10 miles north of Dubois, 17.ix.1976, ex fruit galls of *B. occidentalis,* leg. J. C. Roskam.

Material in coll. Rijksmuseum van Natuurlijke Historie, Leiden. Adults slides no. 761101.1—3, 5—9, 11—12, same data as type-material. Second instar larva

slide no. 730411.3, Canada, Br. Columbia, O'Kanagan Valley, 13.viii.1959, ex fruit galls of *B. occidentalis,* leg. C. G. G. J. van Steenis; third instar slide no. 761101.13, same data as type material; pupa slide no. 730413.13, U.S.A., Montana, Bridger Cañon, alt. 1600 m, 16.ix.1905, ex fruit galls of *B. occidentalis,* leg. Blankinship 460.

I have great pleasure in naming this species after prof. dr. C. G. G. J. van Steenis, Rijksherbarium, Leiden. He collected the herbarium specimen of river birch in which I found larvae of this species. Together with *S. betulae* and *S. brevipalpis, S. steenisi* belongs to the "*betulae* species complex". All these species induce fruit galls with window-pits and have larvae with two pairs of rows of dorsal papillae on the A 1—7 segments. *S. steenisi* is the only species of this complex with only one pair of rows of lateral papillae on the thoracic segments and two pairs of rows of ventrals on the abdominal ones. The pupae have short prothoracic horns. Especially in the males the long antennae with very long internodes are remarkable; in females the length of the superior lamella of the ovipositor is just intermediate between *S. betulae* and *S. brevipalpis.*

Only at a very late moment during this study I recognised West-Nearctic midges of fruit galls to be different from East-Nearctic ones. Before my collection trip to the U.S.A. in 1976 I considered all the larvae derived from Nearctic fruit galls to belong to one, very variable, species. After this trip I reared adults of West-Nearctic material. These adults were different from East-Nearctic midges in many characters. Moreover, it was possible to correlate these differences with differences in larval characters. Because the plates of the other *Semudobia* species were completed before I depicted *S. steenisi,* all the figures of this species are united in the final two plates of this paper.

## **Semudobia tarda** sp. nov.

(male: figs. 28, 29, 46, 47; female: figs. 36, 37, 52, 58, 59, 104; imm. stages: figs. 9, 62, 63, 88—94, 99)

Male. — Width of head 1.23 (1.18—1.26) times its height. Antenna (figs. 28, 29) with 2 + 14 segments, its length 2.81 (2.65—2.81) times the width of head; scape ventrally with 3 (2—3) very short, 4 (3—4) lateral and 0 (0—6) dorsal long setae; third flagellomere with its node 1.11 (0.96—1.11) times as long as its diameter; internodes subquadrate to oblong, internode of third flagellomere 0.48 (0.46—0.56) as long as the node. Maxillary palp 0.28 (0.24—0.28) times the width of head, third segment 0.85 (0.74—0.88) times as long as second. Fronto-clypeal setae 3 (2—3); setae on mesanepisternum absent, 3 (3—7) setae on mesanepimeron. Wing length 1.9 (1.5—1.9) mm, 2.1 (2.1—2.2) times as long as wide; R5 2.4 (2.1—2.5) times as long as R1; Sc indicated by 5 (5—7) sensory-pores, 4 (4—6) sensory-pores on basal part of R1 and 2 on distal part, 3 pores on medio-distal portion of R5. Tibia of hind leg 0.96 (0.76—0.99) times as long as femur, and second tarsal segment 0.53 (0.47—0.55) times this length; fifth tarsal segment 0.79 (0.74—0.88) times as long as fourth. Distimere (fig. 46) rather inflated, 0.48 (0.48—0.49) times as long as basimere; inferior lamella about half-way narrowly V-shapedly incised

(fig. 47); aedeagus rather slender, a little longer than the rectangular, distally emarginated and often heavily chitinized claspettes.

Female. — Width of head 1.25 (1.23—1.30) times its height. Antenna (figs. 36, 37) with 2 + $12^+$ (11—13) segments, its length 1.76 (1.67—1.98) times the width of head; scape ventrally with 2 (2—3) very short, 1 (1—4) lateral and 1 (0—3) dorsal long setae; third flagellomere with its node about as long as (1.00 (1.00—1.08) times) its diameter. Maxillary palp (fig. 104) 0.24 (0.24—0.29) times the width of head; third segment 1.12 (1.00—1.27) times as long as second. Fronto-clypeal setae 2 (0—4); setae on mesanepisternum absent or indistinct, 6 (4—6) setae on mesanepimeron. Wing length 2.1 (1.8—2.1) mm, 2.1 (2.1—2.2) times as long as wide; R5 2.4 (2.3—2.4) times as long as R1; Sc indicated by 4 (4—6) sensory-pores; 4 (4—6) sensory-pores on basal part of R1 and 2 on distal part, 3 pores on medio-distal portion of R5. Tibia of hind leg 0.94 (0.91—0.94) times as long as femur and second tarsal segment 0.51 (0.47—0.52) times this length; fifth tarsal segment about as long as fourth. Tergum 8 triangular (fig. 52), the height of this sclerite about equal to its width. Ovipositor (fig. 59) 1.31 (1.09—1.31) times as long as hind femur, for one-third to about half-way retracted into the eighth abdominal segment; oviduct surrounded by a remarkably chitinized vaginal furca; superior lamella 1.5 (1.5—1.6) times as long as high; inferior lamella very short and truncate (fig. 58).

Immature stages. — Egg length $\bar{n}$ 255 μ, $\bar{n}$ ± 2 SD (95% of egg lengths) between 235—275 μ; width $\bar{n}$ 72 μ. First instar larva (figs. 62, 63); length 255 (212—539), width 97 (85—303) μ; width of head-capsule 29 (26—34), between antennae 12 (11—14) μ, n = 17; dorsal spinule-rows 2 (2—0) + 8 (6—8), ventrals 1 (2—0) + 7 (6—7), n = 10; respiration apneustic. Second instar (fig. 88); length 632 (506—1248), width 269 (237—679) μ; width of head-capsule 65 (47—71), between antennae 17 (17—22) μ, n = 14; dorsal spinule-rows 0 (—1) + 5 (0—8), ventrals 0 (0—2) + 11 (9—11), n = 10. Third instar (fig. 89—91); length 1596 (948—1691), width 1185 (711—1185) μ; width of head-capsule 73 (59—90), between antennae 19 (19—28) μ, n = 31; spathula sternalis large, bilobed (fig. 92, 93), width of spathula 71 (27—71), height 89 (66—102), distance between points of lobes 47 (20—47), height of lobes 27 (19—27), height of median incision 17 (9—17) μ; n = 10. Pupa length 1627 (1404—1643), prothoracic horns 141 (133—143) and apical papillae 47 (38—53) μ, n = 7; sensory-pores situated laterally of the corresponding papillae of the dorsal row (fig. 94).

Papillary pattern (fig. 24a). Dorsal collar papillae absent, one pair of ventral collar papillae. On thoracic segments one pair of dorsal, two pairs of pleural, and one pair of lateral papillae; on Th 1 one pair of sternal papillae, on Th 2 and 3 one pair of ventrals. On segment A 1—7 only one pair of dorsal papillae, one pair of pleural, lateral and ventral papillae; dorsal papillae are absent on A 8, there is one pair of pleural papillae, one pair of laterals and one pair of ventrals; one pair of terminal papillae on AS.

Gall (fig. 99) length 1.7—2.6 mm, $\bar{n}$ 2.1 mm, width 1.7—2.4 mm, $\bar{n}$ 2.0 mm, n = 20; galling of the fruit; the fruit is button-like swollen, subrotund, wings are completely or nearly completely reduced; window-pit rather indistinct *(B. pubescens).*

Type material. — Holotype ♂, slide no. 760223.11, The Netherlands, Renkum, 15.i.1975, ex fruit galls of *B. pendula.* Allotype ♀, slide no. 760211.2, The Netherlands, Meyendel, 28.iv.1975, ex fruit galls of *B. pubescens,* leg. J. C. Roskam.

Material (all my localities are from The Netherlands) in coll.Rijksmuseum van Natuurlijke Historie, Leiden. Adults slides no. 760223. 9—10, 760211.1 and 11, males with the same data as the holotype, females as allotype. First instar larva slide no. 750519.3 Duivenvoorde, 19.v.1975, ex female catkins of *B. pubescens;* second instar slide no. 750619.4, Meyendel, 22.vi.1972, ex fruit galls of *B. pubescens;* third instar slide no. 751001.2, same locality as second instar, 1.x.1975; pupa slides no. 730402. 4—6, 9, same locality as second instar, 2.iv.1973, leg. J. C. Roskam. As regards the phenology (see below) this species is the latest, hence the name *tarda,* the retarded. In the sense of Hennig (1966), this is the *Semudobia* species with many apomorphic characters. According to Möhn (1955), three pairs of rows of dorsal papillae seem to be most common in gall midge larvae, and one pair of rows in *S. tarda* therefore must be considered apomorphic. This is the only *Semudobia* species with apneustic first instar larvae. The heavily chitinized genital structures, viz., claspettes in male and vaginal furca in female, only occur in this species. In my opinion, these character stages must also be regarded as apomorphic.

## **Semudobia skuhravae** sp. nov.

(male: figs. 26, 27, 48, 49; female: figs. 34, 35, 53, 60, 61, 105; imm. stages: figs. 11—13, 66, 69, 82—87, 96, 100)

Male. — Width of head 1.08 (1.08—1.22) times its height. Antenna (figs. 26, 27) with 2 + 13 (12—13) segments, its length 2.32 (2.26—2.49) times the width of head; scape ventrally with one very short, 3 (2—4) lateral and 0 (0—2) dorsal long setae; third flagellomere with its node 1.21 (1.08—1.26) times as long as its diameter; internodes transverse to subquadrate, internode of third flagellomere 0.31 (0.31—0.41) times as long as the node. Maxillary palp 0.28 (0.23—0.31) times the width of head, length of third segment 1.53 (1.05—1.57) times the length of second. Fronto-clypeal setae 4 (1—5); 8 (0—8), often indistinct, setae on mesanepisternum, 8 (4—9) on mesanepimeron. Wing length 2.14 (2.08—2.14) mm, 2.2 (2.2—2.3) times as long as wide; R5 2.2 (2.2—2.4) times as long as R1; Sc indicated by 6 (6—9) sensory-pores, 7 (5—7) pores on basal part of R1 and 2 on distal part, 3 pores on medio-distal portion of R5. Tibia of hind leg 0.84 (0.79—0.87) times as long as femur and second tarsal segment 0.52 (0.47—0.57) times this length; fifth tarsal segment 0.73 (0.73—0.92) times as long as fourth. Distimere (fig. 48) 0.55 (0.52—0.56) times as long as basimere; inferior lamella for about one-third broadly V-shaped incised (fig. 49); aedeagus usually shorter than the verrucose triangular claspettes.

Female. — Width of head 1.19 (1.09—1.19) times its height. Antenna (figs. 34, 35) with 2 + 12 ($11^+$—13) segments, its length 1.61 (1.61—1.87) times the width of head; scape ventrally with 1 (1—2) very short, 3 (3—4) lateral and 4 (2—9) dorsal setae; third flagellomere with its node 1.08 (1.08—1.18) as long as its diameter,

ultimate flagellomere rounded. Maxillary palp (fig. 105) 0.23 (0.23—0.28) times the width of head; length of third segment 1.33 (1.18—1.69) times the length of second. Frontoclypeal setae 5 (1—7); 6 (1—8), often indistinct setae on mesanepisternum,6 (5—9) setae on mesanepimeron. Wing length 2.14 (2.08—2.14) mm, 2.2 times as long as wide; R5 2.3 times as long as R1; Sc indicated by 4 (4—7) sensory-pores, about 6 pores on basal part and 2 (2—3) on distal part of R1, 3 sensory-pores on medio-distal portion of R5. Tibia of hind leg 0.87 (0.87—0.91) times as long as femur and second tarsal segment 0.54 (0.51—0.55) times this length; fifth tarsal segment 0.79 (0.79—0.85) times as long as fourth. Tergum 8 rectangular to H-shaped (fig. 53). Ovipositor (fig. 61) 0.76 (0.75—0.80) times as long as hind femur, for about one-quarter to half-way retracted into the eighth abdominal segment; vaginal furca not remarkably chitinized; superior lamella 2 times as long as high; inferior lamella rounded, about as long as wide (fig. 60).

Immature stages. — Egg length $\bar{n}$ 359 μ, $\bar{n}$ ± 2 SD (95% of egg lengths) between 335—383 μ, width $\bar{n}$ 115 μ. First instar larva (figs. 66—69); length 333 (261—612), width 103 (97—339) μ; width of head-capsule 29 (26—37), between antennae 17 (12—17) μ; dorsal spinule-rows 4 (3—4) + 8 (7—8), ventrals 4 (3—4) + 7 (7—8), n = 10; respiration metapneustic. Second instar (fig. 82); length 679 (442—1059), width 332 (221—727) μ; width of head-capsule 67 (48—79), between antennae 21 (16—26) μ, n = 39; dorsal spinule-rows absent, ventrals 0 (2—0) + 6 (6—8), n = 10. Third instar (fig. 83—85); length 1675 (1138—2022), width 932 (758—1329) μ; width of head-capsule 85 (67—112), between antennae 23 (23—34) μ, n = 41; spathula sternalis extremely variable (figs. 86, 87), more or less bilobed with a variable number (0—6) of small teeth between the usually larger, pointed, lobes, width of spathula 17 (17—44), height 14 (14—20), distance between points of lobes 11 (11—35), height of lobes 3 (3—9), height of smaller, median teeth 2 (2—3) μ, n = 10. Pupa length 1547 (1117—1786), prothoracic horns 114 (114—160) and apical papillae 42 (38—60) μ, n = 10; sensory-pores between the corresponding papillae of the second and third pairs of dorsal rows (fig. 96).

Papillary pattern (fig. 24e). One pair of dorsal collar papillae and two pairs of ventral collar papillae on SS (only visible in first instar). On thoracic segments two pairs of dorsal papillae, two pairs of pleurals, two pairs of laterals; on Th 1 one pair of sternal papillae and on Th 2 and 3 one pair of ventrals. On segments A 1—7 three pairs of dorsal papillae, one pair of pleurals, one pair of laterals, two pairs of ventral papillae; on A 8 one pair of dorsal, one pair of pleural, one pair of lateral, and one pair of ventral papillae; 2—3 pairs of terminal papillae on AS.

Gall (fig. 100) length 1.4—2.0 mm, $\bar{n}$ 1.8 mm, width 1.0—1.2 mm, $\bar{n}$ 1.1 mm, n = 20; galling of the "bract"; the ovoid gall is situated between the spindle of the catkin and the scale; window-pit absent *(B. pubescens).* In Japanese (Honshu, Azegate, *B. ermanii*) and American (South Dakota, Black Hills, *B. occidentalis*) material *S. skuhravae* is found in fruit galls. These galls have no window-pit and are coalescent with the scale. When gall and scale are separated, the membraneous cocoon of the larva becomes visible.

Type material. — Holotype ♂, slide no. 760223.4, Allotype ♀, slide no. 760209.1, The Netherlands, Renkum, 15.i.1975, ex bract galls of *B. pendula,* leg. J. C. Roskam.

Material (all my localities are from The Netherlands) in coll. Rijksmuseum van Natuurlijke Historie, Leiden. Adults slides no. 760223.3, 5—6, 750115.2—3, 760209.2, 760216.2, same data as type material. First instar larva slide no. 750519.6, Duivenvoorde, 19.v.1975, ex catkins of *B. pubescens;* second instar slide no. 750619.7, same locality as first instar, 19.vi.1975, ex bract galls of *B. pubescens;* third instar slide no. 720713.2, Meyendel, 13.vii.1972, ex bract galls of *B. pubescens.* Pupa slide no. 730328.2—3, same locality as third instar, 28.iii.1973, leg. J. C. Roskam.

This species is named after dr. Marcelá Skuhravá, Prague, Czechoslovakia. She was first (Skuhravá & Skuhravý, 1960, 1963) in suggesting the species to be different from *Semudobia betulae,* remarking the correlation of this midge with the bract gall. Moreover she was the first to depict the spathula. In this species all three pairs of rows of dorsal papillae are developed on A 1—7, and so it is most similar to the usual state of papillary pattern in Cecidomyiidae (Möhn, 1955). Because all other *Semudobia* species have less than three pairs of rows, three pairs of rows of dorsal papillae must be considered a plesiomorphic character. On the ventral surface of larvae of *S. skuhravae* the papillary pattern is also very complete: always two pairs of rows of lateral papillae on thoracic segments and two pairs of rows of ventrals on the abdomen. In my opinion these characters of lateral and ventral papillae must be considered a primitive condition in the genus. If we combine the plesiomorphic characters with character states of other semaphoronts, we must conclude that relatively big eggs (this results in a relatively small number of egg per female: about 50 in *S. skuhravae,* about 120 in *S. tarda*) may also indicate a primitive condition. In this way, the galling of the bract may be a primitive condition, too. In adults the situation is more problematic. Gagné (1976) stated that a relatively large number of flagellomeres should be an apomorphic character. In *Semudobia* relatively large numbers of flagellomeres occur in *S. skuhravae,* with plesiomorphic characters in the larval papillary pattern, and in *S. steenisi,* which shares apomorphic characters with *S. betulae* and *S. brevipalpis* in the larval stages.

## DISTRIBUTION

*Semudobia* midges depend entirely on *Betula* species. Therefore, their geographical distribution must be expected to be wholly or partially the same as that of *Betula. Betula* occurs in the whole boreal and temperate part of the Holarctic region (Meusel et al., 1965). For such a huge area, even after years of sampling, the picture can only be very incomplete. Therefore, many more data are needed to get a true understanding of the distribution of *Semudobia* species. Much material for the present study was collected in western Europe. A collecting trip to the U.S.A. resulted in many data on the distribution of *Semudobia,* especially in the Black Hills and the Rocky Mountains. During a year, a graduate student had the opportunity to study insects of birch catkins in Japan. Several samples of birch catkins were collected by colleagues in Canada and Eastern Russia. Finally, many of the present data are based on infections found in plant specimens from the collections of the Rijksherbarium, Leiden and the Herbarium Vadense, Wageningen.

| | | | *S. skuhravae* | *S. tarda* | *S. betulae* | *S. brevipalpis* | *S. steenisi* |
|---|---|---|---|---|---|---|---|
| America | East-Canada | Montreal | - | - | - | + | - |
| | | Ontario | - | - | + | + | - |
| | | Quebec | - | + | - | + | - |
| | West-Canada | Alberta | + | - | - | - | - |
| | | Br. Columbia | - | - | - | - | + |
| | East-U.S.A. | Connecticut | + | - | - | + | - |
| | | Pennsylvania | - | - | + | + | - |
| | | Washington DC | - | - | - | + | - |
| | West-U.S.A. | Colorado | + | - | - | - | + |
| | | Montana | + | + | - | - | + |
| | | South Dakota | + | - | - | - | - |
| | | Wyoming | + | - | - | - | + |
| Europe | Austria | | + | + | + | - | - |
| | Belgium | | + | + | + | - | - |
| | Czechoslovakia | | + | + | + | - | - |
| | Denmark | | + | + | + | - | - |
| | France | | + | + | + | - | - |
| | Germany | | + | + | + | - | - |
| | Great Britain | | + | + | + | - | - |
| | Ireland | | + | + | + | - | - |
| | The Netherlands | | + | + | + | - | - |
| | Norway | | + | + | + | - | - |
| | Poland | | + | + | + | - | - |
| | Soviet-Union | Latvia | + | + | + | - | - |
| | Sweden | | + | + | + | - | - |
| | Switzerland | | + | + | + | - | - |
| Asia | Japan | | + | + | + | - | - |
| | Soviet-Union | Baikal Lake | + | - | - | - | - |
| | | Kamtschatica | - | - | + | - | - |
| | | Kirgistania | + | + | + | - | - |
| | | Nerchinsk | + | - | - | - | - |
| | | Wladiwostok | + | + | + | - | - |

Table 1. Geographical distribution of *Semudobia.*

Table 1 shows a mainly Palaearctic distribution for *S. betulae* and *S. tarda.* When I collected these gall midges in the U.S.A., this was always on introduced European *B. pendula.* Also in Canada, where *S. betulae* and *S. tarda* were collected on *B. populifolia* and *B. papyrifera,* respectively, an introduction of infected fruits of Palaearctic birch species is supposed.

In North America two species of the "*S. betulae* complex" are present: *S. brevipalpis* in the eastern states of Canada and the U.S.A.; *S. steenisi* in the western states including Rocky Mountains. A similar vicariance occurs in the host plant. European *Betula pubescens* is replaced in eastern North America by *B. papyrifera* and in western North America by *B. occidentalis.* The vicariance in

| Station | | number of galls | % infected fruits | *S. betulae* | *S. tarda* | *S. skuhravae* | *S. betulae* ÷ *S. tarda* |
|---|---|---|---|---|---|---|---|
| a | | | | | | | |
| Kootwijk | 1 | 199 | 1.22 | 155 | 10 | 34 | 15.50 |
| | 2 | 715 | 1.30 | 614 | 101 | – | 6.08 |
| | 3 | 495 | 2.75 | 418 | 40 | 37 | 10.45 |
| | 4 | 2945 | 5.26 | 2397 | 248 | 300 | 9.67 |
| | 5 | 369 | 5.58 | 253 | 112 | 4 | 2.26 |
| | 6 | 126 | 0.72 | 110 | 3 | 13 | 36.67 |
| Meyendel | 1 | 486 | 5.31 | 293 | 125 | 68 | 2.34 |
| | 2 | 545 | 5.50 | 226 | 159 | 160 | 1.49 |
| | 3 | 2323 | 15.43 | 2100 | 204 | 19 | 10.29 |
| Duivenvoorde | | 2045 | 9.11 | 905 | 551 | 589 | 1.64 |
| Binnen-Buiten Liede | | 1174 | 6.15 | 753 | 337 | 84 | 2.23 |
| Nieuwkoop | | 5742 | 11.82 | 3099 | 2259 | 384 | 1.37 |
| Ilperveld | 1 | 1011 | 5.10 | 468 | 537 | 6 | 0.87 |
| | 2 | 842 | 2.66 | 454 | 386 | 2 | 1.18 |
| b | | | | | | | |
| Kootwijk | 1 | 138 | 0.37 | 110 | 24 | 4 | 4.58 |
| | 2 | 558 | 1.24 | 370 | 80 | 108 | 4.63 |
| | 3 | 161 | 0.28 | 124 | 12 | 25 | 10.33 |
| | 4 | 367 | 0.71 | 264 | 98 | 5 | 2.69 |
| | 5 | 1210 | 2.54 | 1035 | 164 | 11 | 6.31 |
| | 6 | 190 | 0.70 | 172 | 6 | 12 | 28.67 |
| Meyendel | 1 | 1374 | 5.72 | 833 | 443 | 98 | 1.88 |
| | 2 | 1042 | 3.53 | 795 | 223 | 24 | 3.57 |
| | 3 | 5752 | 10.87 | 3777 | 1709 | 266 | 2.21 |
| Duivenvoorde | | 3274 | 4.70 | 873 | 2310 | 91 | 0.38 |
| Binnen-Buiten Liede | | 949 | 2.43 | 386 | 518 | 45 | 0.75 |
| Nieuwkoop | | 5312 | 6.13 | 2329 | 2853 | 130 | 0.82 |
| Ilperveld | 1 | 3817 | 6.43 | 1770 | 2041 | 6 | 0.87 |
| | 2 | 875 | 1.98 | 325 | 533 | 17 | 0.61 |

Table 2. Occurrence of *Semudobia* species in different study areas during the year 1976. a, early spring; b, late summer.

eastern Asia of *B. pubescens* by *B. davurica* seems not to have been followed by a vicariance in *Semudobia:* all Japanese and East-Russian specimens of *S. betulae* (as are those of *S. tarda* and *S. skuhravae*) are very similar to the European material.

It is of interest to note that *S. betulae* and *S. tarda* both are gall inducers in birch fruits; they usually may be found together in the same birch populations. If different habitats are sampled, the two species seem to be ecologically different. In 1976, the frequency of occurrence of *Semudobia* species in fourteen birch populations of six areas was determined (Table 2). In each population about eight trees were marked; in each sampling series a constant number of catkins were collected. Two series were made, where possible from the same trees, one in early spring just before the emergence of the midges and one in late summer, when infections caused by this generation of midges could be easily recognised.

The study areas. — Kootwijk (52.11 N 5.46 E) is a very dry sandy area where *B. pendula* is abundant. Meyendel (52.08 N 4.20 E) is a dune area with a rather heterogeneous structure: *B. pendula* can usually be found on relatively dry sand dunes, whereas *B. pubescens* is common in the wetter valleys. Duivenvoorde (52.06 N 4.24 E) is a rather wet area, overgrown with blackberry brakes and rushes; of the two birch species, *B. pubescens* dominates here. Binnen-Buiten Liede (52.23 N 4.41 E), Nieuwkoop (52.10 N 4.50 E), and Ilperveld (52.29 N 4.58 E) are very wet bogs; here again, *B. pubescens* is the dominant birch species. In the dry habitat Kootwijk populations, 78% or more of the fruit infections is caused by *S. betulae* (except Kootwijk 5, a young population). In wetter habitats (Duivenvoorde, Liede, Nieuwkoop and Ilperveld), the *S. tarda* part of the fruit infections, especially in the "b" series, is relatively large (44% or more). In the "scattered" Meyendel area both infection "types" are represented with *S. betulae* predominant; there is no distinct correlation with a wet or a dry habitat.

In Switzerland five birch populations at different altitudes were studied. In the areas Kerenzerberg (47.07 N 9.08 E, alt. 600 m), Walenstadtberg (47.08 N 9.18 E, alt. 800 m) and Boggenberg (47.06 N 9.01 E, alt. 1250 m) *S. betulae, S. tarda* and *S. skuhravae* were all common; in the area Ahornen (47.05 N 9.00 E, alt. 1400 m), *S. tarda* was absent and at Stausee Garichte (46.57 N 9.06 E, alt. 1600 m), *S. betulae* was the only gall-inducing midge.

Latitude offers a similar pattern. In Norway, galls were collected in nine areas, varying in North latitude from 58.33 to 64.30. In the two most northern localities, Tunnsjö (64.45 N 13.00 E, alt. 750 m) and Kongsvoll (63.33 N 9.24 E, alt. 1000 m), only *S. betulae* was present. In most other localities, both *S. skuhravae* and *S. betulae* were common. The localities of this series where *S. tarda* was also present are Åseral (58.33 N 7.24 E, alt. 250 m) and Ossjoën (61.20 N 11.30 E, alt. 500 m).

The reason why *S. tarda* is absent at high altitudes and/or latitudes may be a phenological one. *S. tarda* is the latest in pupation (pag. 181); for this species the vegetation period in these extreme areas may be too short to complete larval development.

The southern-most locality in western Europe, where *Semudobia* infections were found, is Saintes in France (45.45 N 0.45 W); *S. betulae* and *S. tarda* both are abundant there. In Japan the most southern locality is Honshu, Azegate (36.44 N 139.27 E, alt. 1280 m); there *S. skuhravae* is the only gall inducer.

In Europe, *S. betulae, S. tarda* and *S. skuhravae* regularly occur together; this seems to be different in the Nearctic Region. In Canada and the U.S.A. 20 infected birch populations were sampled (populations with introduced Palaearctic species excluded). In only 6 populations *S. skuhravae* was found together with either *S. brevipalpis* or *S. steenisi;* in 7 populations *S. skuhravae* was the only gall inducer, in 4 populations this was *S. brevipalpis* and in 3 populations *S. steenisi.* It is of some interest to mention that in one large area (Black Hills, South Dakota) four birch populations (*B. occidentalis* and *B. papyrifera*) could be detected with *Semudobia* infections. In all these cases *S. skuhravae* was the only gall inducer.

## LIST OF HOST PLANTS

Besides the fresh material, about 300 herbarium specimens with fruit catkins were investigated on *Semudobia* infections. Kuzneva (in Komarov, 1936), Rehder (1940), and Ohwi (1965) were used for the identification of birch taxa. The nomenclature is according to Kruessmann (1960) and Fontaine (1970). The taxa are listed in Table 3. Absence of infections by certain gall midge species of taxa marked by an asterisk may be due to the small sample size.

The genus *Betula* may be divided into four sections. The section Acuminatae is exclusively East Asiatic. The section Costatae has a disjunct areal: some of the species are East Asiatic, other species are only found in the eastern part of North America. The section Excelsae is Holarctic and the section Humiles is mainly Circumpolar. None of the species belonging to the section Acuminatae were infected at all. In the section Costatae infections are mainly common in the East Asiatic species: *B. costata, ermanii, grossa, jacquemontii* and *raddeana;* here, *S. skuhravae* is the most common gall inducer. In East American *B. alleghaniensis* infections occur, but they are very rare (*S. skuhravae,* one gall in one cultivated specimen only). The absence of infections in *B. lenta* may be explained by the very typical odour of the cherry birch, which may act as a repellent compound for *Semudobia.* Also in the section Humiles, *S. skuhravae* seems to be the predominant species. *B. nana* deserves special attention. Bachmaier (1965) reported that infections of *Semudobia* are not rare. In more than 30 specimens, however, I found only one single gall of *Semudobia* in a Norwegian sample. In Einsiedeln, Switzerland (47.07 N 8.45 E, alt. 900 m), a heather with *B. nana* is mixed with and surrounded by normally infested *B. pubescens;* although flowering times of *B. nana* and *B. pubescens* coincide (Hegi, 1957), no infections of *Semudobia* were found in those dwarf birches. In Åseral, Norway (58.33 N 7.24 E), a bog with *B. nana* mixed with *B. pubescens* and their hybrid *B.* × *intermedia* was visited. Both *B. pubescens* and *B.* × *intermedia* were crammed with *Semudobia* infections. Here, again, not a single gall was found in *B. nana.* Finally, infections are common in most species of the section Excelsae.

## PHENOLOGY

In The Netherlands (Meyendel), the respective ontogenetic stages were observed in the following periods of 1976 (Table 4). In fig. 25, some differences in

| Section | Species | *S. skuhravae* | *S. tarda* | *S. betulae* | *S. brevipalpis* | *S. steenisi* |
|---|---|---|---|---|---|---|
| Acuminatae | ★*B. alnoides* Buch.-Ham. | – | – | – | – | – |
| (Regel). | ★*B. cylindrostachya* Lindl. apud Wallich | – | – | – | – | – |
| | *B. maximowicziana* Regel | – | – | – | – | – |
| Costatae | ★*B. albo-sinensis* Burkill | – | – | – | – | – |
| (Regel). | *B. alleghaniensis* Brit. | c | – | – | – | – |
| | ★*B. corylifolia* Regel & Maxim. | c | – | – | – | – |
| | *B. costata* Trautv. | + | + | – | – | – |
| | *B. ermanii* Cham. | + | c | c | – | – |
| | *B. forrestii* (W.W.Sm.) Hand.-Mazz. | – | – | – | – | – |
| | *B. grossa* Sieb. & Zucc. | + | c | – | – | – |
| | *B. jacquemontii* Spach. | c | – | c | – | – |
| | *B. lenta* L. | – | – | – | – | – |
| | ★*B. medwediewii* Regel | – | + | – | – | – |
| | ★*B. nigra* L. | – | – | – | – | – |
| | ★*B. raddeana* Trautv. | c | – | c | – | – |
| | ★*B. schmidtii* Regel | – | – | – | – | – |
| | *B. utilis* D. Don | + | + | – | – | – |
| Excelsae | ★*B. chichibuensis* Hara | – | – | – | – | – |
| (Koch). | ★*B. x coerulea* Blanchard | c | c | – | – | – |
| | ★*B. coerulea-grandis* Blanchard | c | – | – | – | – |
| | ★*B. celtiberica* Rothm. & Vasc. | – | – | – | – | – |
| | *B. davurica* Pall. | – | – | – | – | – |
| | *B. x intermedia* (Hartm.) Thomas | + | – | + | – | – |
| | ★*B. kirghisorum* Sav. | + | + | + | – | – |
| | ★*B. litwinowii* Doluch. | c | – | c | – | – |
| | *B. occidentalis* Hook. | + | – | – | – | + |
| | *B. papyrifera* Marsh. | + | c | c | + | – |
| | *B. pendula* Roth | + | + | + | – | – |
| | *B. platyphylla* Suk. | + | + | + | – | – |
| | *B. populifolia* Marsh. | c | – | c | + | – |
| | *B. pubescens* Ehrh. | + | + | + | – | – |
| | ssp. *carpathica*, ssp. *murithii* | + | + | + | – | – |
| | ★*B. turkestanica* Litv. | + | – | – | – | – |
| Humiles | ★*B. apoiensis* Nakai | – | – | – | – | – |
| (Koch). | *B. x borggraveana* Zabel | c | – | c | – | – |
| | ★*B. fruticosa* Pall. | + | – | – | – | – |
| | ★*B. glandulifera* (Regel) Butler | – | – | – | – | – |
| | *B. glandulosa* Michx. | + | – | – | – | – |
| | *B. humilis* Schrank | c | + | + | – | – |
| | ★*B. middendorffii* Trautv. | – | – | c | – | – |
| | *B. nana* L. | (+) | – | – | – | – |
| | *B. pumila* L. | + | – | – | – | – |
| | ★*B. x purpusii* Schneid. | – | – | – | – | – |
| | ★*B. tatewakiana* M. Ohki & S. Watanabe | – | – | – | – | – |

Table 3. List of host plants. + infections under natural conditions; c, infections in plants, cultivated outside their distribution area, e.g. botanical gardens; (*) less than 5 specimens studied.

phenology of the Palaearctic species are demonstrated. *S. skuhravae* is the earliest species to pupate, *S. tarda* the latest; *S. betulae* is the first in passing the first and second stages.

Effects of different altitudes on phenology were studied in Switzerland. In Walenstadtberg (alt. 800 m), situated on a sunny slope above the Walensee, no remarkable differences with The Netherlands (Meyendel), were found. On

Table 4. Phenology of Palaearctic *Semudobia* species.

| stage | period |
|---|---|
| third instar larva | until 12.iv |
| pupa | 15.iii — 1.v |
| adult | 20.iv — 9.v |
| egg | 28.iv — 15.v |
| first instar larva | 8.v — 23.vi |
| second instar larva | 9.vi — 12.vii |
| third instar larva | from 16.vi |

Boggenberg (alt. 1250 m), *Semudobia* appears about three weeks later, but in Ahornen (alt. 1400 m) and at Stausee Garichte (alt. 1600 m) no eggs were observed before the end of May, and at the end of July only first and second instar larvae were found. Third instar larvae were collected in the last week of August at Ahornen and Stausee Garichte.

Similar effects on the phenology are observed at high latitude. In the first half of July, 1976, infections of *Semudobia* were observed in eight areas in Norway (61.20 N — 64.30 N). Most localities are situated at about 950 m alt. In six areas only first instar larvae were present at that date; in only two cases, Ossjoën (61.20 N 11.30 E, alt. 500 m) and Rindal (63.05 N 8.30 E, sea level), also second instar larvae could be collected.

The full-grown larva of *Semudobia* undergoes diapausis; it is impossible to rear adults unless they have passed a cold period. In one case (Wyoming, Wind River), larvae of *S. steenisi,* collected in September, 1976, and, transferred to my room, pupated and gave rise to adults in the beginning of October. A similar absence of diapausal condition must have occurred in the material of Forsius (1927), who got adults in August.

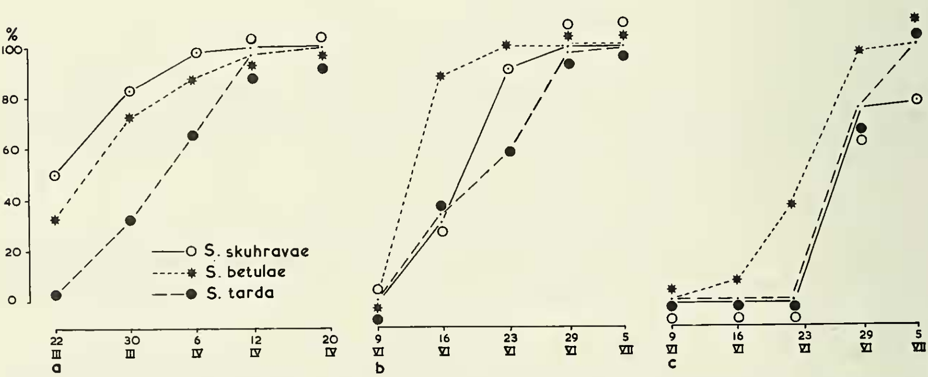


Fig. 25. Phenology of *Semudobia*. a, % pupated midges; b, % animals that passed first stage moulting; c, % animals that passed second stage moulting.

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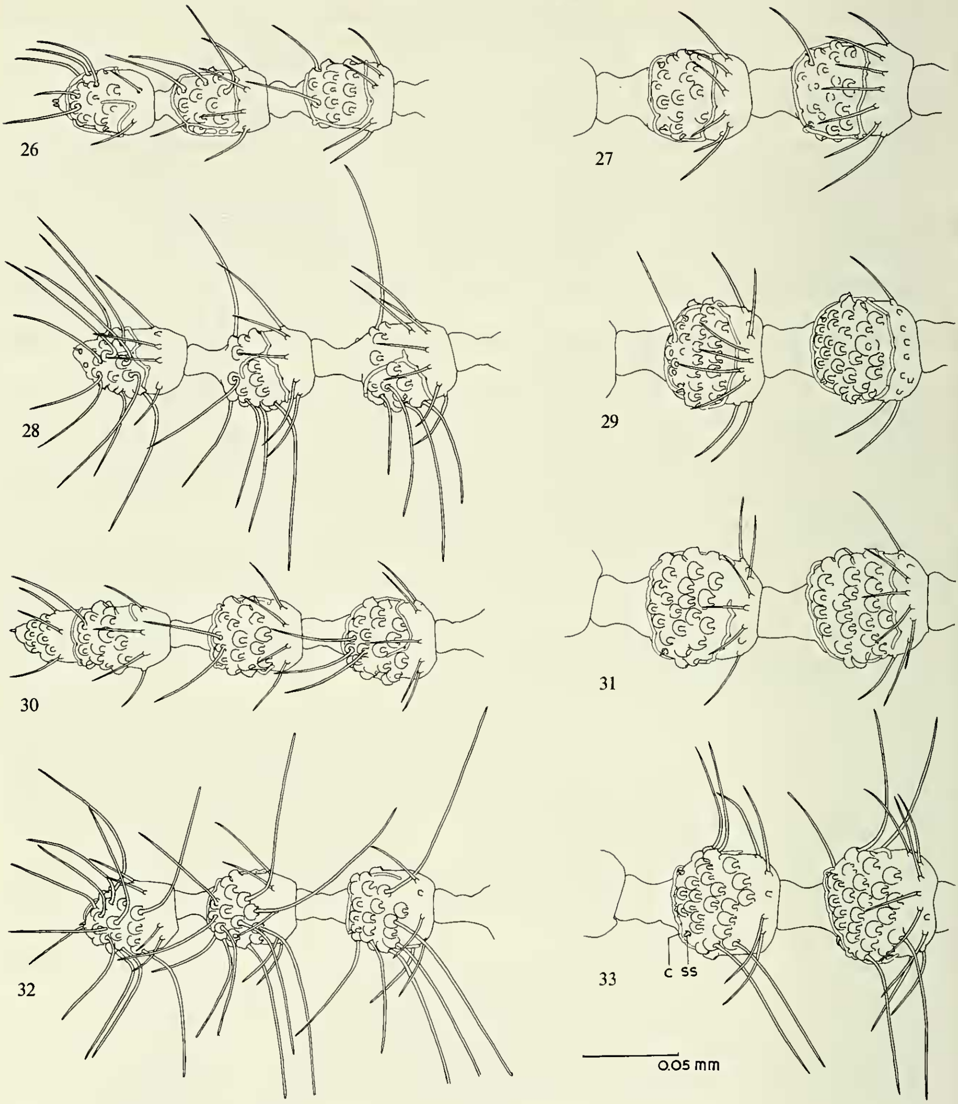
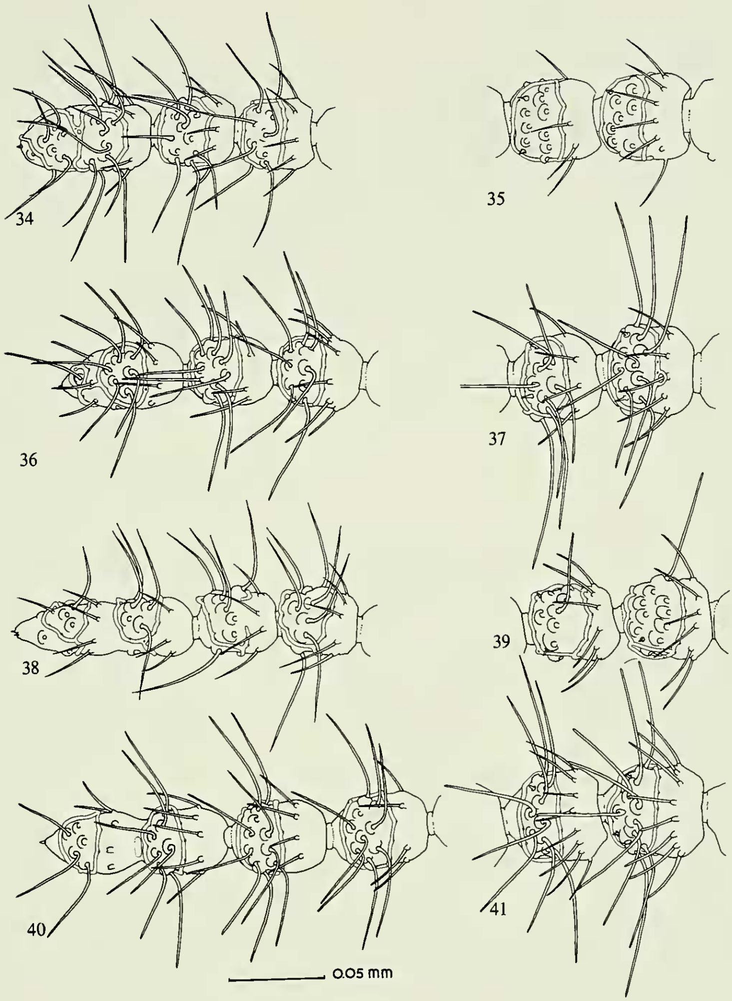
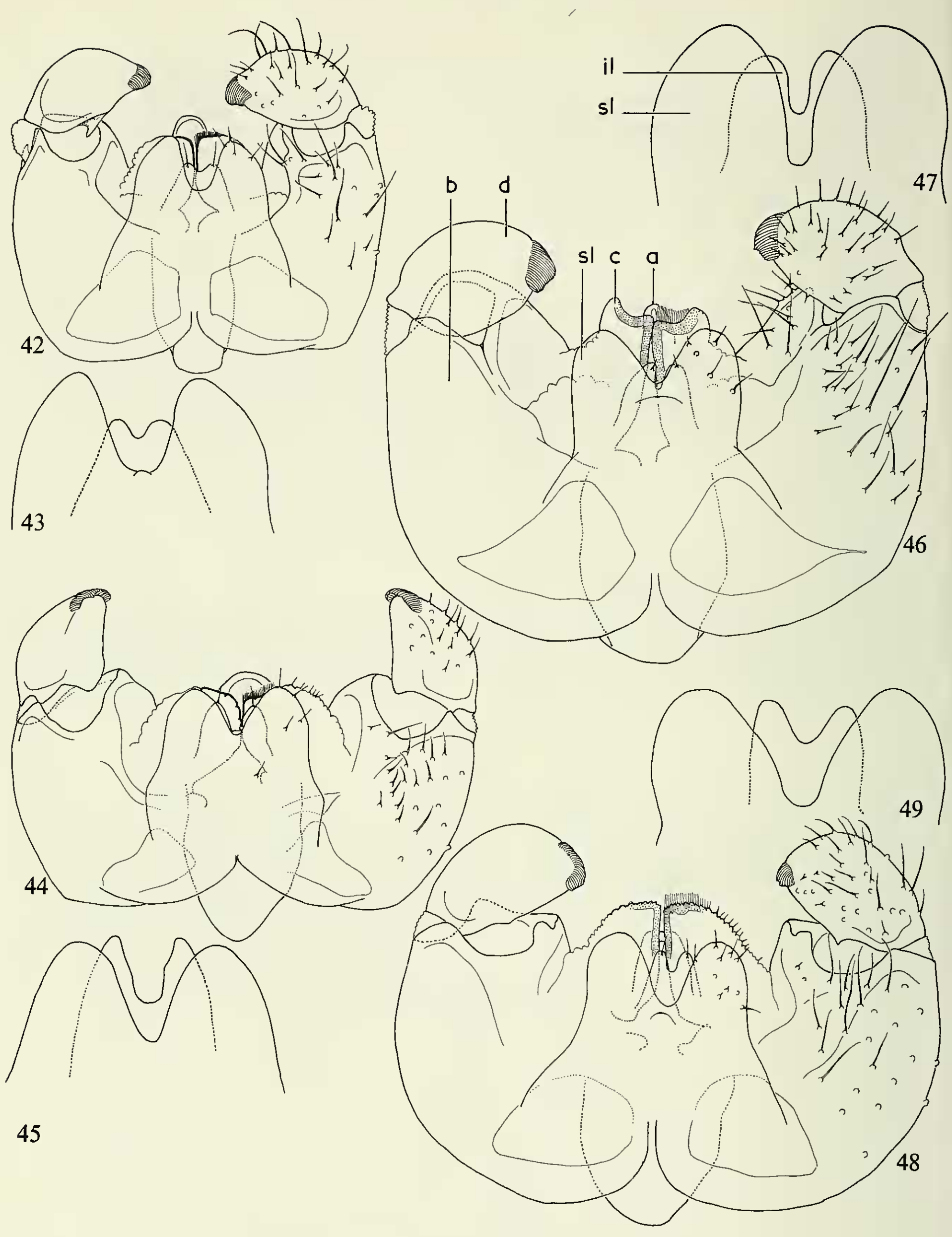


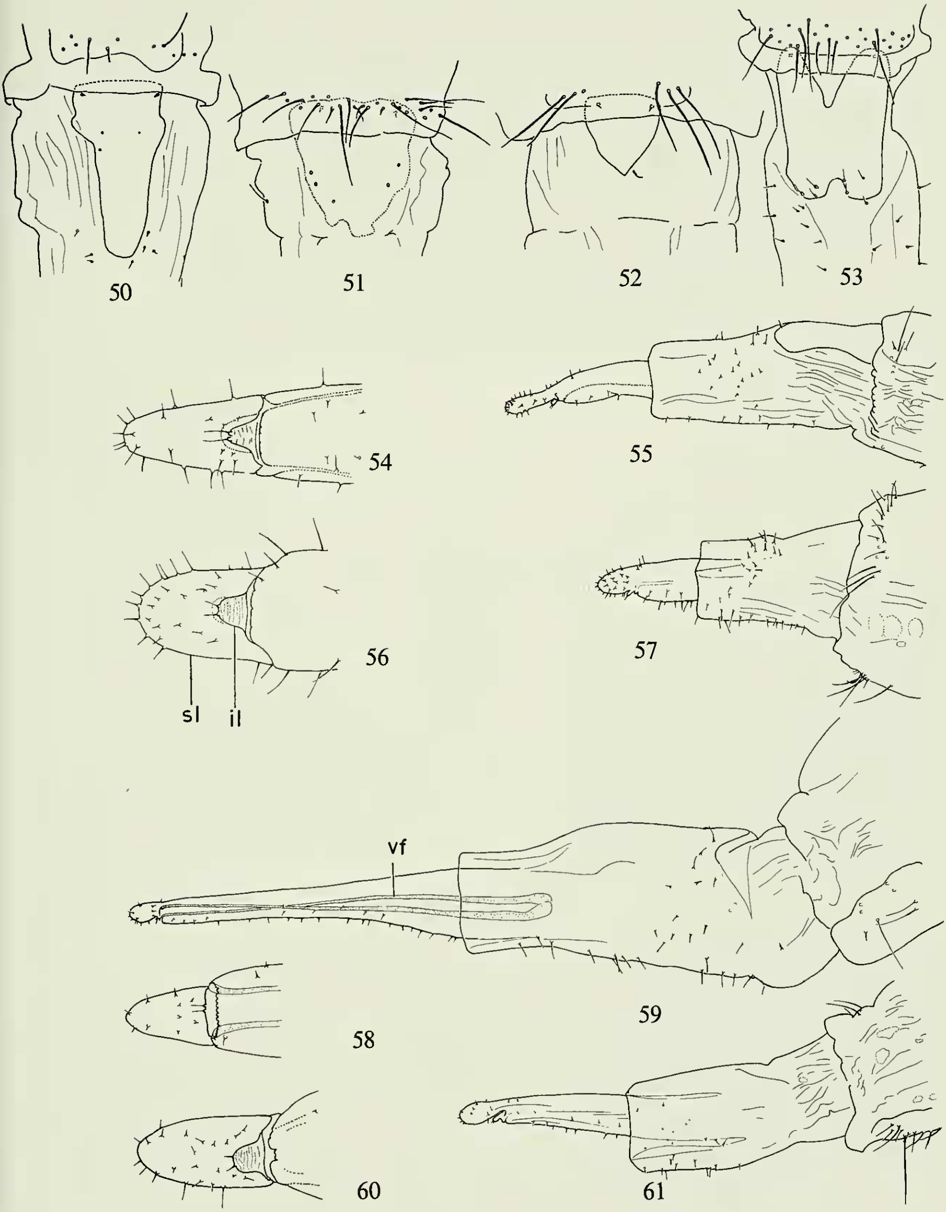

Figs. 26—33. Fifth, sixth and ultimate antennal segments, ♂. 26—27, *S. skuhravae*; 28—29, *S. tarda*; 30—31, *S. brevipalpis*; 32—33, *S. betulae*. c, circumfila; ss, sensorial spine.



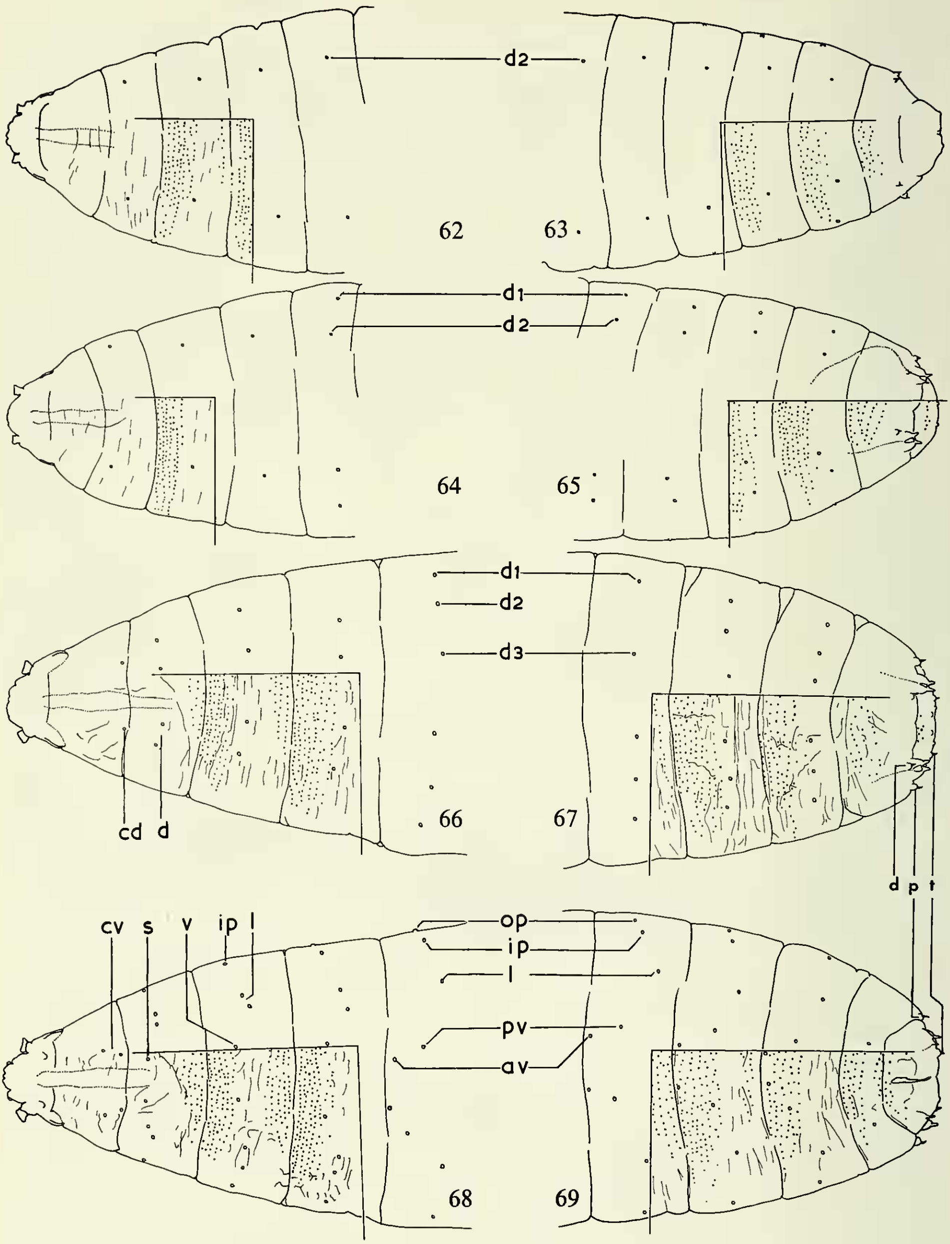

Figs. 34—41. Fifth, sixth and ultimate antennal segments, ♀. 34—35, *S. skuhravae*; 36—37, *S. tarda*; 38—39, *S. brevipalpis*; 40—41, *S. betulae*.



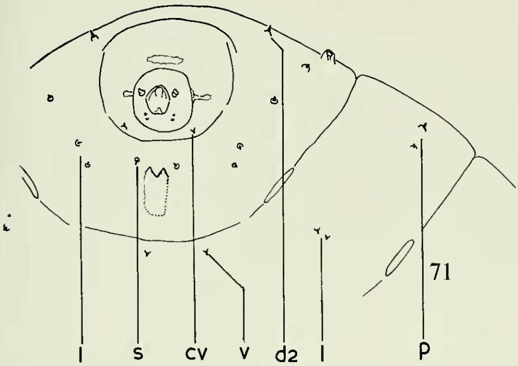

Figs. 42, 44, 46, 48, male genitalia, dorsal aspect; 43, 45, 47, 49, detail of superior and inferior lamella: 42—43, *S. betulae*, 44—45, *S. brevipalpis*, 46—47, *S. tarda*, 48—49, *S. skuhravae*. a, aedeagus; b. basimere; c. claspette; d, distimere; il, inferior lamella; sl, superior lamella. 42, 44, 46, 48, × 220; 43, 45, 47, 49, × 400.




Figs. 50—53, female eighth tergum; 54, 56, 58, 60, detail of female superior and inferior lamella, ventral aspect; 55, 57, 59, 61, ovipositor, lateral aspect: 50, 54, 55, *S. betulae*; 51, 56, 57, *S. brevipalpis*; 52, 58, 59, *S. tarda*; 53, 60, 61, *S. skuhravae*. il, inferior lamella; sl, superior lamella; vf, vaginal furca. 50—53, × 120; 54, 56, 58, 60, × 260; 55, 57, 59, 61, × 85.




Figs. 62—69. First instar larva. 62, 64, 66, head and thorax, dorsal aspect; 68, ditto, ventral aspect; 63, 65, 67, sixth to eighth abdominal segment and anal segment, dorsal aspect; 69, ditto, ventral aspect: 62—63 *S. tarda*; 64—65 *S. betulae*; 66—69 *S. skuhravae*; av, anterior ventral papilla; cd, dorsal collar papilla; cv, ventral collar papilla; d, d1—3, dorsal papilla; ip, inner pleural papilla; l, lateral papilla; op, outer pleural papilla; p, pleural papilla; pv, posterior ventral papilla; s, sternal papilla; t, terminal papilla; v, ventral papilla. × 400.

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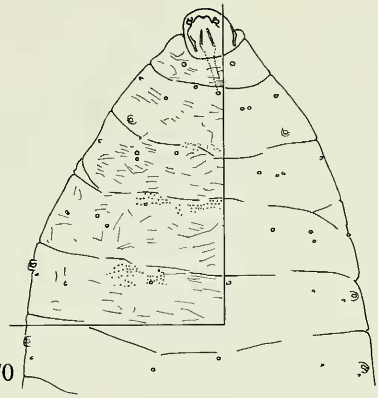

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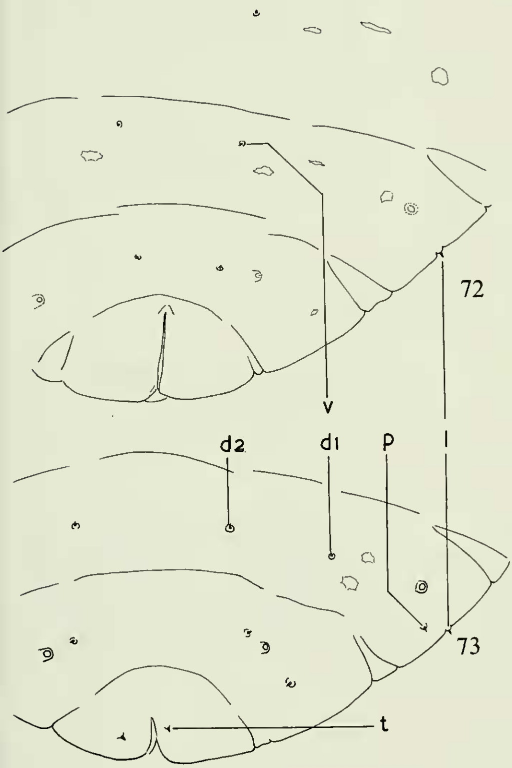


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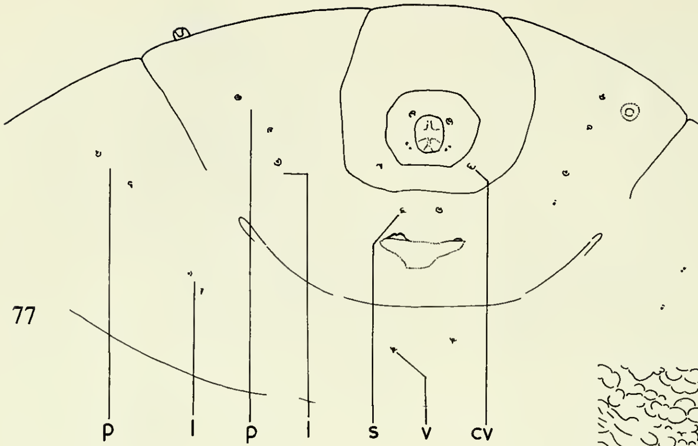
Figs. 70—75. *S. betulae*. 70, head and thorax of second instar, ventral aspect; 71, head, supernumerary segment and first thoracic segment of third instar, ventral aspect; 72, seventh and eighth abdominal segments and anal segment of third instar, ventral aspect; 73, ditto, dorsal aspect; 74—75, spathula sternalis: 74, The Netherlands, Meyendel, 75, Kamtschatca. For explanation of symbols, see figs. 62—69. 70—73, × 140; 74—75, × 425.

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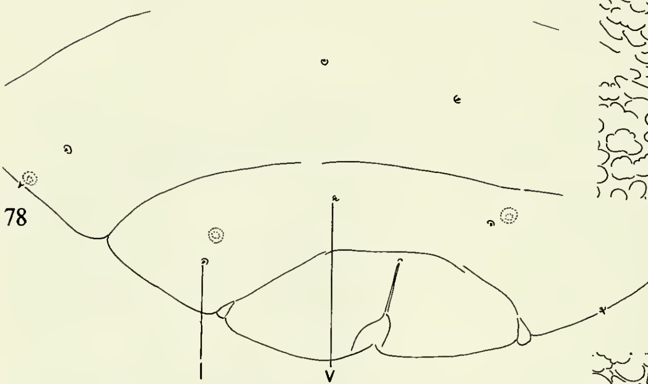


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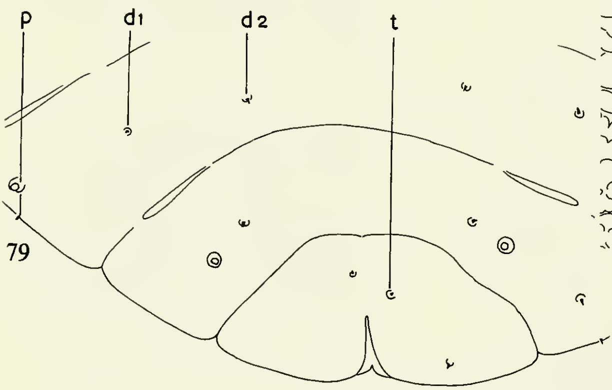


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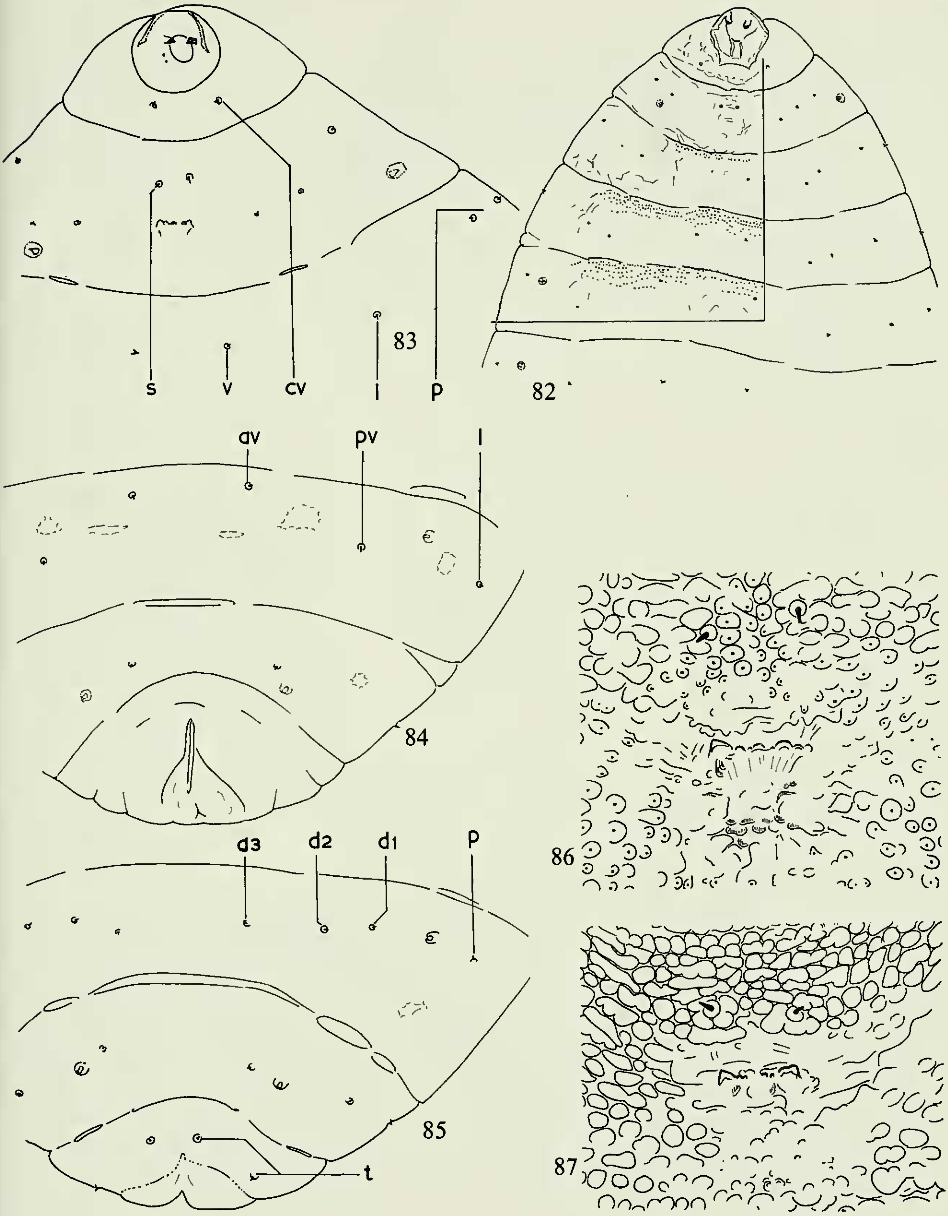
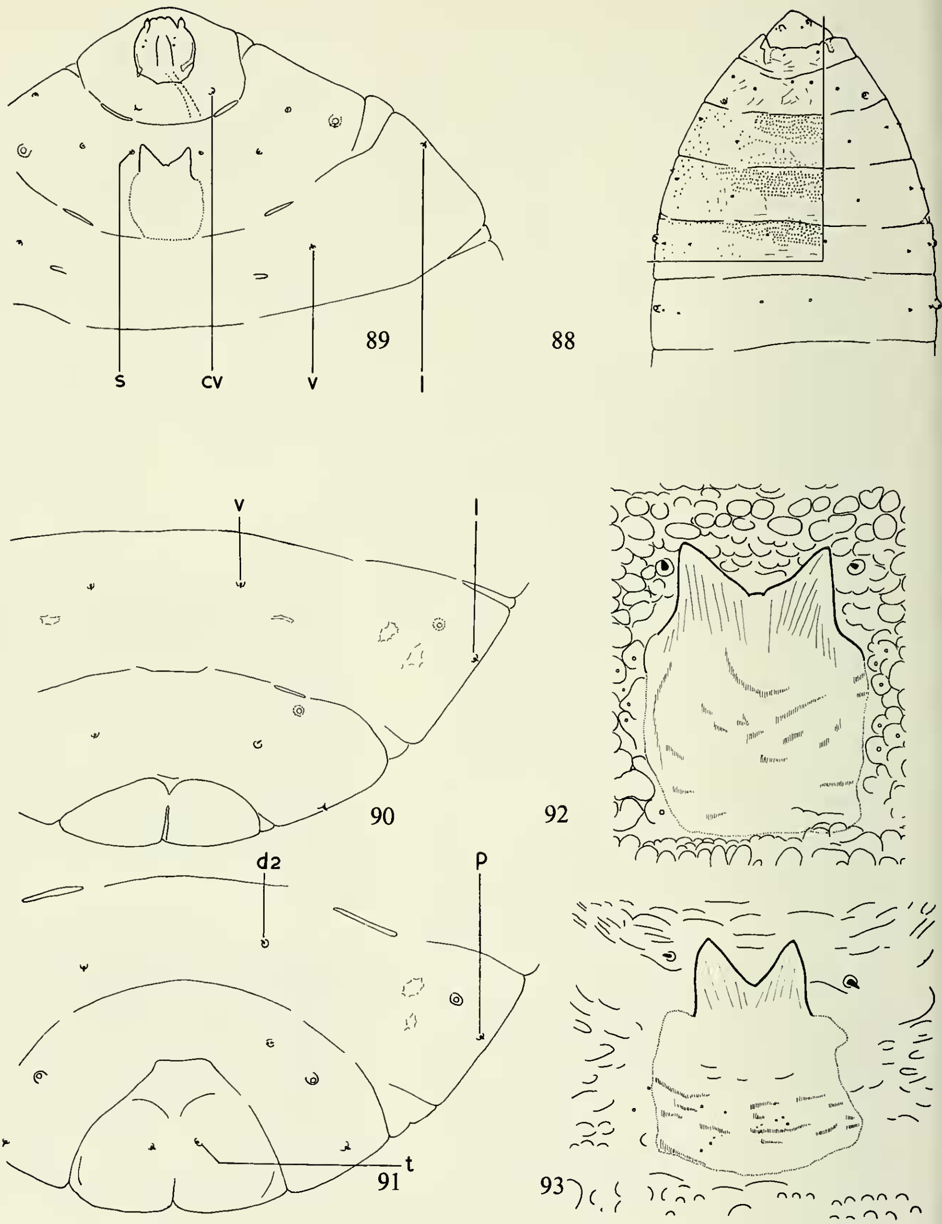
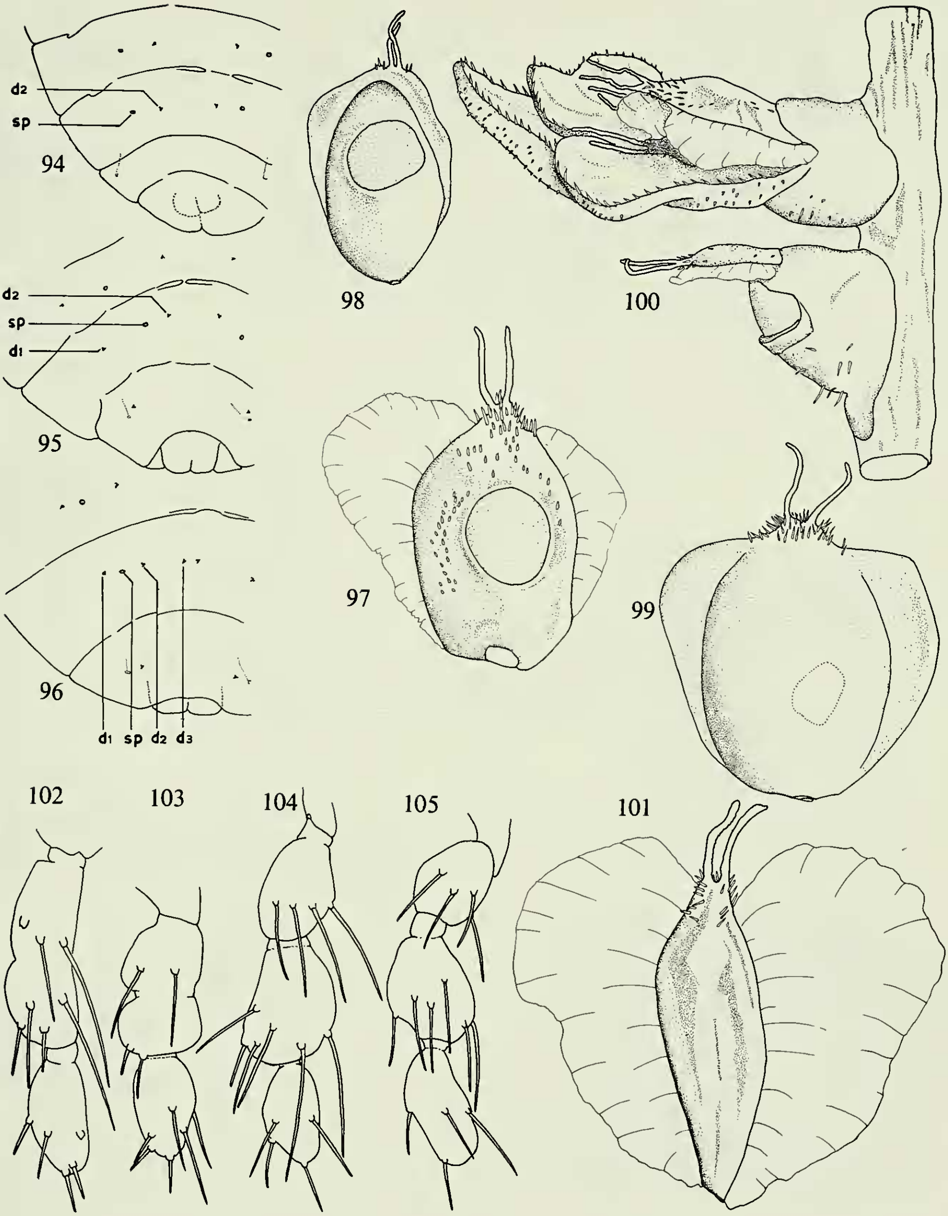
Figs. 77—81. *S. brevipalpis*. 77, head, supernumerary segment and first thoracic segment of third instar, ventral aspect; 78, seventh and eighth abdominal segments and anal segment of third instar, ventral aspect; 79, ditto, dorsal aspect; 80—81, spathula sternalis: 80, U.S.A., Washington DC., 81, Canada, Quebec. For explanation of symbols, see figs. 62—69. 77—79, × 140; 80—81, × 425.



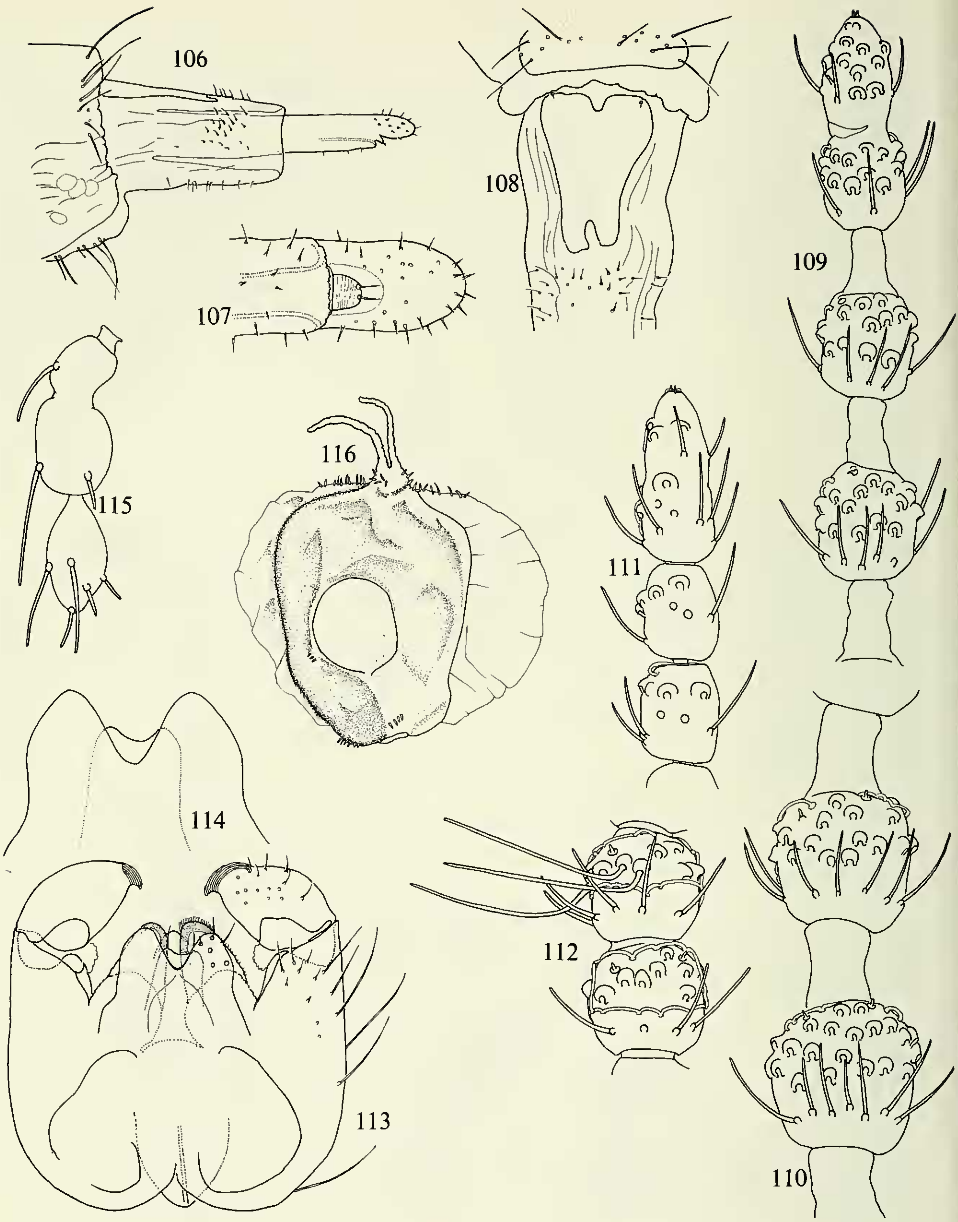

Figs. 82—87. *S. skuhravae*. 82, head and thorax of second instar, ventral aspect; 83, head, supernumerary segment and first thoracic segment of third instar, ventral aspect; 84, seventh and eighth abdominal segments and anal segment of third instar, ventral aspect; 85, ditto, dorsal aspect; 86—87, spathula sternalis: 86, The Netherlands, Meyendel, 87, Canada, Alberta. For explanation of symbols, see figs. 62—69. 82—85, × 140; 86—87, × 425.



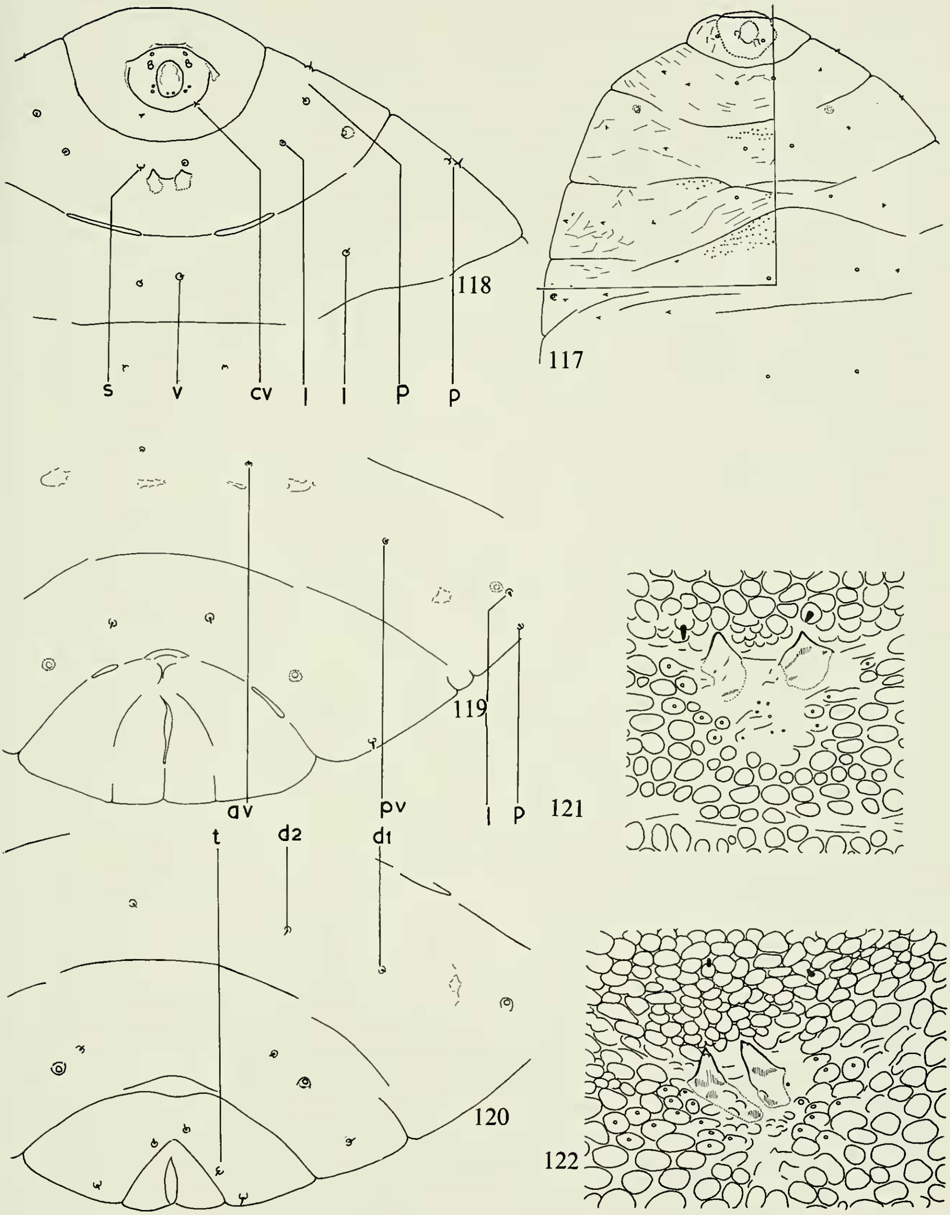

Figs. 88—93. *S. tarda*. 88, head and thorax of second instar, ventral aspect; 89, head, supernumerary segment and first thoracic segment of third instar, ventral aspect; 90, seventh and eighth abdominal segments and anal segment of third instar, ventral aspect; 91, ditto, dorsal aspect; 92—93, spathula sternalis: 92, The Netherlands, Meyendel, 93, Japan, Sapporo. For explanation of symbols, see figs. 62—69. 88—91, × 140, 92—93, × 425.




Figs. 94—96, seventh and eighth abdominal segments of pupa, dorsal aspect; 97—100, gall; 101, healthy fruit of *Betula pendula*; 102—105, female maxillary palp: 94, 99, 104, *S. tarda*; 95, 97, 102, *S. betulae*; 98, 103, *S. brevipalpis*; 96, 100, 105, *S. skuhravae*. d1—3, dorsal papilla; sp, sensory-pore. 94—96, × 75; 97—101, × 13; 102—105, × 400.




Figs. 106—116. *S. steenisi*. 106, ovipositor, lateral aspect; 107, detail of female superior and inferior lamella, ventral aspect; 108, female eighth tergum; 109, male ultimate antennal segments; 110, male fifth and sixth antennal segments; 111, female ultimate antennal segments; 112, female fifth and sixth antennal segments; 113, male genitalia, dorsal aspect; 114, detail of male superior and inferior lamella; 115, female maxillary palp; 116, gall. 106, × 85; 107, 114—115, × 400; 108, × 120; 109—112, × 330; 113, × 220; 116, × 13.




Figs. 117—122. *S. steenisi*. 117, head and thorax of second instar, ventral aspect; 118, head, supernumerary segment and first thoracic segment of third instar, ventral aspect; 119, seventh and eighth abdominal segments and anal segment of third instar, ventral aspect; 120, ditto, dorsal aspect; 121—122, spathula sternalis: 121, Canada, Br. Columbia, 122, U.S.A., Montana. For explanation of symbols, see figs. 62—69. 117—120, × 140; 121—122, × 425.